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Abstracted by Nils Holmgren, author
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Points of view concerning forebrain morphology in lower vertebrates.

This paper contains an attempt to show that the pallium of practically all vertebrates is divided into three parts, known from reptiles and mammals as hippocampal, general pallial, and pyriform cortex. This opinion is founded especially on the conditions in embryonic shark brains. This same subdivision is also demonstrated in ganoids and bony fishes, where the so-called striatum is shown to contain these same parts. The everted forebrain of bony fishes is explained as resulting from a preceding phylogenetic inverted and evaginated stage. Also to the subpallial parts author has paid attention and attempted to establish the homologies through the series of lower vertebrates. The paper ends with a part treating with the forebrain phylogeny in the light of paleontology. The paper deals in more detail with the forebrains of Petromyzon, Acanthias, Chimera, Protopterus, Polypterus, Lepidosteus, Amia, Acipenser, and Teleosts.

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POINTS OF VIEW CONCERNING FOREBRAIN MORPHOLOGY IN LOWER VERTEBRATES

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FORTY-TWO FIGURES (NINE PLATES)

For some years I have been occupied with investigations upon the brain structure of different vertebrates. I have paid much attention to the morphology of the forebrain, which seems to me not sufficiently understood by former workers. I have thus made extensive studies on this part of the brain in Myxine and bony fishes. In addition, I have made studies on Petromyzon, selachians, holocephalians, ganoids, amphibians, reptiles, and mammals, studies which, however, have not yet resulted in publications, but have nevertheless given many valuable points of view concerning forebrain morphology, some of which are subjects of special investigations at this institute and under my direction.

In vertebrates there are two different types of forebrain present, the everted and the inverted. The everted is confined to Polypterus, ganoids, and teleosts, the inverted to all other vertebrates. The essential difference between these two types is, that in the former the dorsal walls of the forebrain are bent outward, while in the latter they are bent inward so as to form the roof of the brain. In the everted forebrain the roof is made up by the greatly expanded tela.

Concerning the inverted type, it may be accentuated that the process of inversion, that takes place in a very early embryonic stage and is very soon followed by an evagination process, results in the formation of the hemispheres. This evagination process not only widens the brain cavity in the lateral direction, but also evaginates the lateral ventricles forward and backward to form

the anterior and the posterior horns (if present) of the lateral ventricles. The anterior ventricle extends into the olfactory bulb and forms the ventricle of the bulb. Through the inversion the dorsal parts of the embryonic lateral plates of the forebrain rudiment ('Anlage') not only are brought in contact with each other, but also are sometimes bent down parallel with each other to form in the roof an incomplete septum, dorsal to the foramen monroi, between the lateral ventricles. Through the anterior evagination, parts of the brain vesicle, which hitherto were situated on the lateral side, are brought into medial position in front of the lamina terminalis to form a forward continuation of the imperfect dorsal septum mentioned above. The anterior septum will thus be complete. As there is in the forebrain vesicle a roof- and a floor-part, the perfect septum must be composed of corresponding parts: the roof-part is the medial part of the archipallium (if differentiated), the floor-part is the paraterminal body or septum pellucidum of the authors. The limit between the floor-part and the roof-part is in many cases a very distinct one, a zona limitans (in teleosts, selachians, ganoids, amphibians, reptiles, birds, and perhaps also in mammals). It seems to be very unnecessary to make these statements made several times before, but in a recent paper Lundahl has declared that the septum pellucidum (paraterminal body) is a pallial structure, that he names palaeopallium. This curious view, which is not consistent with well-known facts, seems to fall to the ground in view of the above statements concerning the evagination of the hemispheres.

As to the everted brain type, it may be accentuated that this is surely not primary in character, but rather to be derived from an inverted and evaginated type. This seems to be evident a priori from the fact that the brain of the lower vertebrates (cyclosomes, selachians) is inverted; and also in the organization of the everted brain there are present the most distinct signs of its origin from an inverted type. I will call attenton at once to the fact that in ganoids and certain bony fishes (Lophius, Anguilla) there is a ventricle in the olfactory bulb. This ventricle is continued backwards by a groove which caudad decreases

in distinctness. This groove undoubtedly represents the remains of a previous lateral ventricle and represents the sulcus limitans externus, whose most characteristic feature is its leading out into the bulbar ventricle.

In Acipenser and other cartilaginous ganoids the eversion of the telencephalon is very much less pronounced than in bony ganoids and teleosts, and the bulbar ventricle is much greater. This fact seems to point in the direction that the inversion is a primary character of the forebrain of fishes. The same conclusion must be drawn from the fact that the forebrain vesicle of a young embryo of Lepidosteus is very clearly inverted.

After these introductory notes, we will turn attention to the pallial structures. What is, then, the pallium in the morphological sense? It is not easy to define this idea in a manner to include therein the pallium of all vertebrates. It seems not to be possible to accept the definition of Edinger and others, whose opinion is that a true pallium (Episphaerium = Neencephalon) does not receive olfactory fibers of lower order than the third. I cannot accept this view, since it supposes that a brain nucleus would not be able to change its connections without changing its morphological value. It is a well-known matter of fact that the connections of a nerve-nucleus can change in different closely related species (for instance, the nucleus rotundus in bony fishes). But none will for that reason declare that this nucleus is not a homologous one. While the hind part of the roof of telencephalon in selachians is said not to receive olfactory fibers of the second order,[1] but only such of the third, the conclusion is not at all justified that this hind part has a quite different morphological value than the anterior part of similar construction, but with secondary olfactory tracts ending therein. In such a case the conclusion indicated by the facts is that a process of differentiation has taken place in such a manner that the brain roof (the pallium) has become divided into two parts, of which the one is connected with secondary olfactory fibers, the other with tertiary. The morphological unity of the roof remains nevertheless as before.

[1] My studies have shown that this is a false statement, as there are really olfactory fibers of the second order ending in the posterior part of the pallium.

A subdivision of the telencephalon into a hyposphaerium and an episphaerium, of which the hyposphaerium receives secondary olfactory fibers, the episphaerium tertiary, seems not to be a good morphological subdivision. How, then, shall we make a morphological subdivision of the forebrain, how delimit the pallial structures from the subpallial? I think that the morphological ground for such a separation is given in the presence of the fovea limbica and the sulcus limitans externus, or better the sulcus limitans pallii (if present) on the lateral side of the brain-wall and the sulcus limitans medialis and the sulcus limitans (Elliot Smith) on the medial side and, of course, in the presence of the zonae limitantes, those sharply defined, cell-free zones which cut through the brain-wall in the neighborhood of the above-mentioned sulci. All *parts dorsal to the zonae limitantes belong to the pallium, the parts ventral thereto are subpallial.* This definition coincides essentially with that given by Herrick,[2] but he has not used the zona limitans as limit, but taken an imaginary line connecting the fovea limbica with the sulcus limitans externus and the sulcus limitans medialis with the sulcus limitans (Elliot-Smith). Sometimes this imaginary line coincides with the zona limitans, sometimes it falls a little ventral to the zona. This difference seems to be of very little practical importance and in cases where the zona is lacking, the imaginary line will serve as well as a zona.

CYCLOSTOMATA

Petromyzonts

The forebrain of Petromyzon is very clearly inverted, but the medial borders of the inverted parts do not reach each other. Thus a pallial septal structure does not occur. Lateral ventricles are evaginated cephalad in the olfactory bulb, caudad in the 'olfactory lobe.' In adult Petromyzon ventricular grooves are absent, but in the larva there is a distinct sulcus limitans externus (fig. 1, *s.l.e.*) leading cephalad into the bulbar ventricle.

[2] For literature see the list in my paper: Zur Anatomie und Histologie des Vorder- und Zwischen-hirns der Knochenfische. Hauptsächlich nach Untersuchungen an Osmerus eperlanus. Acta Zoologica, vol. 1, 1920, pp. 137–315.

Through this sulcus the pallial parts of the brain are approximately separated from the subpallial. The pallium is medially bordered by the primordium hippocampi of Johnston (praethalamus of other authors, fig. 2, *p.h.*). I wish not to express any definite opinion as to this primordium hippocampi. Johnston's opinion is founded on the behavior of the velum transversum, but there seems to be some analogy between the primordium hippocampi and the eminentia thalami of amphibians, especially in the relations to the taenia bundles. Also the embryological development of this hippocampal formation is not convincing to the advantage of Johnston's interpretation. For the 'primordium hippocampi' of the Ammocoetes-larva of 30 mm. is an ependymal border of the medial pallium—a border that insensibly passes over into the ependymal roof of the brain-vesicle (fig. 2, *p.h.*). Later the primordium grows thicker (fig. 3A) as the taenia bundles enter it, and it becomes ganglionic. The fact that the 'primordium hippocampi' is situated before the point of lateral attachment of the velum transversum is not a fact of definite importance, since there is no ground present why the di-telencephalic border should be a straight line behind the 'primordium hippocampi' and not a bent line before this part of the brain. A comparison between figures 3A and 3B, respectively from Ammocoetes and Triton, reveals so great concordance that I find the opinion of the 'primordium hippocampi' as a part of thalamus comparatively well settled.

I thus regard as the pallium of Petromyzon what Edinger calls the lobus olfactorius. In the cephalic part of this lobus olfactorius he observed a small dorsomedial part, which he thought to be an 'Episphaerium-Anlage' (fig. 4, "*Ep.*"). This part is a great olfactory glomerulus with dorsocaudal situation in the olfactory bulb. (In the figure in his 'Vorlesungen,' which illustrates the 'Episphaerium' rudiment, the 'primordium hippocampi' of Johnston is falsely labeled 'ganglion habenulae.')

In the pallium there is present a cortical layer of propyramidal cells (fig. 2, *Cort. I*). This layer is somewhat diffusely composed, but nevertheless very conspicuous. It is laterally somewhat subdivided, but the subdivisions have rather the appearance of

detached cell-groups than of special cortical areas. Thus one can state for Petromyzon that there is a cortical layer present extending from the ventro-lateral part of the pallium to the medial. Such a cortex I would be very inclined to call a palaeocortex, but this term is preoccupied by Kappers in another sense.

At the ventricular wall there is a second layer of cells, forming a ventricular cortical sheet (fig. 2, *Cort. 2*).

The entire hemisphere receives secondary olfactory fibers from the olfactory bulb, but the pallial part receives also tertiary olfactory tracts from the subpallial part of the forebrain. There is no part present exclusively arranged for the reception of the tertiary tracts only. Under the exterior cortical layer there is a stratum containing unmedullated fibers.

The limit between the pallial part and the subpallial is not marked by a zona limitans, but nevertheless the limit is very conspicuous, the cells on the opposite sides of the limit being of different dimensions, the dorsal larger, the ventral smaller, but more densely crowded.

In the subpallial part it is impossible to distinguish different subdivisions in the arrangement of the cells. The entire basal part of the brain acts as a tuberculum olfactorium + striatum + nucleus taeniae, but no one of these parts is differentiated.

Is the forebrain of Petromyzon of ancestral type? Almost every account of forebrain phylogeny begins with the petromyzonts as having the most primitive structure of all living vertebrates. This conception is to some degree justified by the, in many respects, ancestral character of these animals and also by some features in the forebrain morphology, the forebrain being more simply built up than in other vertebrates. There are no special subpallial nuclei and the pallium is uniformly constructed. But are these features sufficiently significant to allow the conclusion that the entire forebrain is of an ancestral type? I think not, and I will now try to show that such a presumption is not very well founded. I will try to show that the forebrain of Petromyzon is secondarily reduced.

The ventricular system of Petromyzon consists of a medial unpaired ventricle from which the lateral ventricles rise. Each

lateral ventricle splits up into two parts, a rostal and a caudal one. The first is the ventricle of the olfactory bulb (fig. 4, *o.v.*) homologous with the same in other animals. The second (figs. 1, 2) has been compared with the lateral ventricle of the hemisphere and regarded as homologous with this. The common aperture of the 'lateral ventricles' into the medial ventricle has been regarded as the foramen monroi. This conception of the Petromyzon forebrain is not allowable, as will be clearly demonstrated by means of an examination of the ventricular system in an Ammocoetes of 1.7-cm. body length. In this stage the forebrain has the same exterior aspect as in more advanced stages and in adult animals, but the ventricles are arranged in another way. The bulbar and the hemispheral ventricle are free from each other (compare figs. 4, 2, and 1), opening into the medial ventricle with separate openings, the bulbar lying ventral to the hemispheral. From the bulbar ventricle a distinct groove runs backwards in the wall of the medial ventricle (fig. 1, *s.l e.*) and a good distance under the opening of the hemispheral ventricle. This groove apparently is the sulcus limitans externus, as pointed out above. This furrow in other vertebrate brains is seen at the lateral wall of the lateral ventricle in various positions in different vertebrates, but always belonging to the lateral wall of the lateral ventricle. According to the current view of the ventricular system in Petromyzon, the sulcus limitans externus here should not belong to the lateral ventricle. It is highly improbable that Petromyzon should in this respect represent a quite different type than all other vertebrates. Thus I am obliged to accept the opinion that the hemispheral ventricle in Petromyzon represents only the dorsolateral part of an ordinary forebrain ventricle This dorsolateral part is tube-like, directed towards the neck part of the pallium, perhaps representing a ventricle analogous to the posterior diverticulum of the forebrain ventricle in Acanthias. Owing to this, it is clear that the foramen monroi of the Petromyzon brain is no true foramen monroi The ventricular system in the forebrain of Petromyzon thus is to be considered as a highly reduced one. This reduced ventricular system indicates that also the entire forebrain is not ancestral, but

secondarily modified. How the primary cyclostome forebrain originally was built up, it is not possible to make out in detail, but that the ventricular system of it was wider, with normal lateral ventricles and a sulcus limitans externus as in other brains, is sure. The general form of such a forebrain may have been more or less like that of selachians with the bulbi olfactori situated lateral at the rostral part of the forebrain vesicle, as in an early embryo. The hemispheres were surely not joined in the dorsal mid-line, where the brain roof consisted of a tela, more or less as in Chimaera. It is a priori probable that the transformation of the exterior of the forebrain was accompanied by transformations in the finer structure, but the nature of these transformations it is not possible to determine. In a young Ammocoetes, however, it is clearly seen that there are two pallial cell-layers present, a peripheral and a ventricular. These layers are in the medial part distinctly separated by a relatively cell-free space. These two layers are also to be distinguished in adult animals, but the cell-free space here is absent. Perhaps the conclusion from this fact may be admitted that there were two cortex layers present in the ancestral cyclostome, as in selachians, Dipnoi, etc., as will be shown later on.

Myxinoids

The conditions in the forebrain of Petromyzon are repeated in Myxine, as I have already pointed out in my memoir on the remarkable brain of this animal (Svenska Vetenskapsakad:s Handlingar, vol. 60, no. 7, 1919). Through the reduction of the ventricle system and the hyperinversion of the pallial parts, the curious aspect characterizing this brain is realized. Here I may only call attention to the fact that the pallium contains a very distinct cortical layer. No zona limitans is present and it is difficult to limit the pallium from the subpallial parts, the cells of both being equal in size and the basal cortical cells flowing over into the subpallial. In the subpallial parts no separate ganglia are to be recognized, as in Petromyzon.

For particulars reference may be made to the above-quoted paper; here it is enough to accentuate that the principles of the brain construction are the same in Myxine and Petromyzon.

SELACHIANS

In selachians the inversion of the forebrain is much more advanced than in Petromyzon, the inverted parts reaching each other in the medial plane and there being bent down and grown together to form the short dorsal septum hanging down between the lateral ventricles in the region of the foramen monroi. The evagination also has a different character than in Petromyzon.

The lateral ventricle is evaginated into the olfactory bulb, which has a lateral situation, but to this there is added an evagination in the rostral direction which causes a ventricular pouch medial to the olfactory crus. In consequence of the latter evagination, brain parts, occupying in other vertebrates a medial position in the septum, should be brought forward and lateralward to cover the topographically foremost part of the brain. Morphologically, the frontal parts of the brain hemispheres thus should belong to the medial side—a matter of fact that should be of some importance in comparing the selachians with other vertebrates. The reason why I have here not followed this scheme is this:

This scheme is only applicable under the presumption that the terminal situation of the olfactory crus is primary. But early ontogenetic stages not only in selachians, but also in cyclostomes, ganoids, teleosts, dipnoans, and amphibians, show that the primary situation of the bulbus is a lateral one and that in these animals except in selachians, the bulbus rudiment is dislocated during ontogeny to a terminal position. As the bulbus rudiment is a subpallial structure, this wandering of the bulbus rudiment is generally effected in the subpallial part without changing the pallial conditions. In early ontogenetic stages the rudiment of the pallial cortex is found medial and in its foremost part rostral to the bulbus rudiment, in the same way as in selachians, as shown below. Thus I consider the selachian condition to be primary; those of the other vertebrates, with the hippocampal formation extending directly to the olfactory crus, as secondary.

The pallial structures in selachians seem to have been very little understood and as to the cortical layers they have been nearly

unknown. I, therefore, here will treat of them at some length. In the adult Acanthias these cortical structures are not very conspicuous, owing to the fact that the cells of the different cortical parts are not very different in aspect; but in embryos of different ages it is very easy to demonstrate that real cortical layers are differentiated. But these structures are already in the postembryo not very conspicuous, owing to the increase of ganglion cells from the ventricular sheet of neuroblastic tissue, and in the adult animals they are scarcely more than indicated by more or less packed cell formations. To make these structures understood it is necessary to follow their embryological development by means of series of different stages.

My material consists of the following stages of the common Squalus acanthias: 3, 3.3, 3.7, 3.8, 3.9, 4, 4.5, 4.9, 5, 6.5, 8, 15 cm. length of the body. The brain was dissected out and cut (15 to 20μ), especially in the transverse direction. Staining with cresyl-violet.

1. Stage of 3-cm. body length. In this stage in the pallial part of the brain the ventricular layer of neuroblastic cells is in great activity forming nerve cells which are pressed outward to form a thick sheet covering the whole dorsal aspect of the ventricle. This layer is not yet delimited from the neuroblastic layer from which it is derived. No differentiation is to be found in this primordial cortex.

In the basal parts of the forebrain the cortex of the tuberculum olfactorium (area superficialis basalis of Johnston) is about to delaminate from the ventricular position in order to form a separate area of cortex-like structure.

2. Stage of 3.3-cm. body length (measured after fixation in Carnoy's fluid). The primordial cortex is in the stage of delamination from the ventricular layer. In the foremost part of the brain the primordial cortex is continuous with the thick ventricular layer, except in its lateral part, where there is a thin cell-free space between it and this layer (fig. 5). The delamination of the dorsal and medial part of the cortex is not so far advanced, but a relatively cell-free space between the cortex and ventricular layer is marked by a sheet of small cell-free spots which are

seen in the sections as a row of white points (fig. 6). Thus the primordial cortex here is practically differentiated as an uninterrupted cortical layer passing from one side of the brain roof over to the opposite. Examining this layer with attention, one cannot avoid observing that the extreme lateral part of it is somewhat different from the remaining. Its cells are a little larger, less densely packed and assume a paler color than the other cortical cells. *In this early stage the differentiation of the pyriform cortex thus is begun.* This pyriform lobe is quite dorsal in position and dorsal also to the olfactory prominence (bulbus olfactorius). Lateral to the pyriform lobe a relatively cell-free space represents an obsolete zona limitans, lateral to which the olfactory bulb rudiment is situated.

It is of some importance to observe that the primordial cortex at one point is continuous with the ventricular layer, viz., the dorsolateral part, medial to and below the pyriform lobe, where cell masses are streaming out from the ventricular layer pressing the primordial cortex against the brain surface and partially coalescing with it. This process represents the first stage of the formation of a new cortical layer, which begins below the medial part of the pyriform cortex and from here extends medially, forming what I will name the general pallium.

In the subpallial parts of the brain the cortex of the tuberculum olfactorium is nearly quite disengaged from the ventricular sheet. The bulbar nuclei are in this stage under formation from the ventricular layer at the lateral part of the ventricle inside the olfactory bulb rudiment (the most lateral part of the forebrain). Between these bulbar nuclei and the upper border of the tuberculum olfactorium cortex there is found a diffuse, in the lateral part rather dense, mass of cells, derived from the underlying ventricular sheet. This cell-mass, I think, represents a lateral olfactory nucleus.

3. Stage of 3.7-cm. body length (measured after fixation in Carnoy's fluid). In this stage the pyriform lobe is separated from the remaining primordial cortex layer, excepting in the foremost part of the brain, where the two cortex components seem to flow together. The part of the ventricular layer from which the

general pallium is under formation is much broader than in the preceding stage and occupies nearly the whole dorsal aspect of the ventricular layer (fig. 7, *g.p.c.*). From this cell-masses are streaming out below the primordial cortex (fig. 8, *prim.c.*), pressing the intermediate part of this cortex (the exterior layer of the general pallium) against the brain surface and partly confluent with it (fig. 8, *g.p.c.*). Since in the foremost part of the brain the lateral and medial parts of the primordial cortex are not exposed to this pressure, the primordial pallium is thus divided into three parts, a medial, a dorsal, and a lateral, respectively corresponding to the hippocampal, the general pallial, and the pyriform cortex, of which the pyriform is formed first. The general pallium (the inner layer) develops after the pyriform lobe and causes a frontal separation of the hippocampal pallium from the pyriform lobe.

The hippocampal part of the primordial cortex rostrally is tolerably well differentiated. At the recessus neuroporicus the hippocampal pallium dorsal to this recess *joins the corresponding part of the other hemisphere.* Caudal to the neuroporic recess the hippocampal part is continuous with that of the other side, forming a thin sheet of cells passing the mid-line close to the ventricular layer. On each side of the mid-line the hippocampal cortex is confluent with the underlying general pallial rudiment. In summary, the hippocampal primordial pallium consists of: 1) a frontal part covering the medial part of the frontal pole of the brain hemisphere; 2) a commissural part dorsal to the recessus neuroporicus.

In the front part of the brain the zona limitans lateralis is well marked. At the extreme lateral part of the forebrain the zona limitans is obsolete and the pyriform lobe is continuous with the lateral olfactory nucleus. Caudal to the bulbus olfactorius rudiment the zona grows more conspicuous.

The evagination of the forebrain in this stage not being more than commenced, the septal structure is very short. The zona limitans medialis is not pronounced and the subpallial parts directly adjoin the hippocampal structure at the upper level of the neuroporic recess. The septum is filled with a dense mass of

cells in which no differentiated nuclei are to be seen. This cell-mass is rostrally continuous with the lateral olfactory nucleus.

The cortex of the tuberculum olfactorium is well developed and caudally merges with the preoptic nucleus or the somatic area of Johnston. The nucleus olfactorius lateralis is denser than in the preceding stage.

4. Stages of 3.8 to 4.5-cm. body length. In the stages of 3.8, 3.9, 4, and 4.5 cm. the development is not much advanced in relation to the stage of 3.7 cm. body length. The brain has grown somewhat larger and the cells migrated from the ventricular layer are more numerous, but the general arrangement is almost the same as before. In the stage of 4.5 cm., however, it is to be noted that the pyriform cortex is much better limited against the ventricular sheet and in the *medial* part of the forebrain also against the general pallium rudiment. In the foremost part of the forebrain, the pyriform cortex and the hippocampal cortex rudiment are everywhere continuous with each other (fig. 9). The *zona limitans lateralis* is very conspicuous in the cephalic part of the brain (fig. 10, *z.l.l*); it grows, however, more indistinct in the caudal part, behind the olfactory bulb rudiment. A *zona limitans medialis* is not to be seen.

5. Stage of 4.9-cm. body length. Of this stage I have had at my disposal only a series of transverse sections which were inclined forward. Thus the cortical parts of the forebrain are not in the same position as in the perfectly transverse sections described before. Therefore, it is somewhat difficult to make an adequate comparison between this stage and the preceding ones. But so much is at once clear, that no greater changes have taken place. The arrangement of the layers is quite the same. The part of the primordial cortex, however, uniting the pyriform lobe with the hippocampal rudiment has grown more conspicuous, a cell-free space in the foremost part of the brain having arisen between this cortex and the general pallial rudiment which now seems to be in rapid development.

The evagination of the forebrain being much more advanced, the septum has increased considerably in length and the septal nuclei are under formation. In the preceding stages the septum

is filled up by an elongate, vertical cell-mass belonging to the nucleus olfactorius lateralis, which basally merges with the tuberculum olfactorium cortex. The cells of this septal nucleus, however, assume a much paler color than the tuberculum cells. In the stage of 4.9 cm. the septal nucleus consists as before of a dense cell-mass on each side of the medial line and begins basally to detach from the tuberculum cortex. Between the two septal nuclei, the mid-part of the septum is filled up by rather scattered cells. Ventrally this cell-lamina spreads out between the medial parts of the tuberculum olfactorium cortex. Against the foramen monroi where the septal nuclei are confluent below the neuroporic recess the vertical cell-lamina disappears, and the basal part of the same is found ventral to the united basal parts of the septal nuclei.

The inversion of the forebrain vesicle is not essentially more advanced than before. The zona limitans lateralis is tolerably well marked, but the zona limitans medialis is not visible at all.

6. *Stage of 5-cm. body length (measured after fixation in Carnoy's fluid).* This stage is much more advanced than indicated by the body length. This was undoubtedly much greater in the living specimens than in the preserved. I think that the difference may be estimated at 3 to 4 mm. in favor of the living specimen.

In this stage the essentials of the pallial structure are differentiated. Therefore I will deal with it in a little more detail than with the preceding stages. I here will adopt the method of describing a number of transverse sections, cut at different levels of the forebrain.

A. Cross-section taken just in front of the foremost part of the lateral ventricle (fig. 11). The wall of the ventricle is just touched by the section. At this level the hemispheres are quite free from each other. The ventricular neuroblastic layer is touched a little below the middle of each hemisphere. Dorsal to this point is a great dense cell-mass, representing the ventricular cell-layer which covers the dorsal portion of the ventricle frontally. Dorsal to this cell-mass is a great cell-free space lying as a

cap on it, and dorsal to this space is seen a dense regular cortical layer (*prim.c.*). This is thicker in its lateral part than in its medial. The cortical layer represents the primordial cortex, the lateral part of which belongs to the pyriform lobe, the medial to the hippocampal rudiment.

Below the ventricle is a clear space crossing over the ventral part of the brain and delimiting the nucleus olfactorius lateralis and the tuberculum olfactorium cortex which lie below it. This space, poor in cells, medially bends up dorsad to the medial border of the hippocampal rudiment. The dorsal part of this clear space in the future development is destined to become the zona limitans medialis (*z.l.m.*). The lateral part of the space in question also bends dorsad to the lateral border of the pyriform lobe and forms the *zona limitans lateralis* (*z.l.l.*). *Thus at the front pole of the forebrain vesicle the zona limitans medialis and lateralis unite.* The above-named cell-free space is present always from the 3.3-cm. stage, but now for the first time it is possible to see the future fate of it.

B. Cross-section taken through the foremost part of the septum (fig. 12). The lateral ventricle is cut in its rostral part, the ventral as well as the dorsal part of the ventricle being opened by the section. The cross-section of the ventricle is more or less S-shaped. The cell-free space below the ventricle has disappeared but the medial and the lateral parts of it are seen as zonae limitantes, of which the medial (*z.l.m.*) is less conspicuous than the lateral (*z.l.l.*). The tuberculum olfactorium cortex covers the whole ventral surface of the section, and is continuous with the septal nucleus mentioned in preceding stages.

In the pallial part of the forebrain the pyriform lobe (*p.c.*) occupies the lateral part and consists of a lateral rounded cell-mass, that sends a cortical lamina in the medial direction parallel to the dorsal surface of the brain vesicle. This cortical lamina is medially continued by a thin sheet of scattered cells (*sc.c.*) which medially merges with the hippocampal rudiment (*h.c.*). The lamella of scattered cells representing the outer layer of the general pallium is the backward extension of the cortical part connecting in the preceding sections the pyriform lobe with

the hippocampal. In the section before us this connection is nearly broken off. This condition probably is the consequence of the development of the inner general pallial cortex (*g.p.c.*). In the preceding stages this cortex was quite ventricular in position. Now it is separated from the ventricle by a cell-poor space and has assumed the characters of a thick special cortical layer. The preparations give the impression that the growth of this cortex should be the reason for the breaking of the primordial connection between the hippocampal and the pyriform cortex. Below the general pallium the ventricular neuroblastic layer seems to be in activity, forming new nerve cells, but the activity is not very rapid (the ventricular cell-layer having not increased much during the period from 5- to 6.5-cm. body length) except at one point, viz., medially below the hippocampal rudiment. Here there is a very pronounced emigration of cells (*h.em.*) towards this rudiment. The hippocampal rudiment in this section appears as a nearly vertical, short lamella (*h.c.*) of densely packed cells. Ventrally this cell formation is limited by the obsolete zona limitans medialis, dorsally it insensibly merges into the above-mentioned lamina of scattered cells, connecting it with the pyriform lobe. Laterally the hippocampal rudiment is continuous with the emigrating cells (*h.em.*) mentioned above.

C. Cross-section through the tip of the recessus neuroporicus (fig. 13). The olfactory bulb rudiment is touched at its cephalic side. The most striking feature of this section is that the pyriform lobe (*p.c.*) is quite dorsal in position. The portion occupying in the preceding section the lateral part of the brain vesicle has disappeared and the corresponding part in this section is filled up by scattered cells. A closer analysis of this field of scattered cells shows that it represents the zona limitans, which has bent upward in such way that it is here cut longitudinally (*z.l.l.*). The upper border of this field lies lateral to the pyriform lobe, and in the consecutive sections the zona here bends caudally again on the lateral border of this lobe, above the olfactory bulb rudiment.

The general pallial cortex (*g.p.c.*) covers the main part of the dorsal aspect of the section. Outside of it there are some scat-

tered cells, remnants of the outer general pallial layer connecting the pyriform with the hippocampal lobe.

The hippocampal rudiment (*h.c.*) consists of a rather dense cell-mass, including the above-mentioned ventricular mass of emigrating cells, and a lamella of scattered cells lying medial to it, continuous with the scattered cells on the surface of the brain.

D. Cross-section 60μ before the foramen monroi (fig. 14). The section touches the front surface of the olfactory bulb recess and passes through the basal portion of the neuroporic process.

In the pallial parts the following changes from the preceding section are to be mentioned.

1. The pyriform lobe is, of course, distinct, but its medial border is confluent with the lateral part of the general pallial cortex.

2. The general pallial cortex has grown thicker in its medial part than in its lateral, so as to form in the cross-section a club-like figure, with the thickening (*g.p.t.*) directed toward the medial line. The medial part of this cortex is bent down a little.

3. At the point where the pallial thickening just mentioned ends we meet with a new cell-mass, emerged from the medial emigration (*h.cm.*) locus of the ventricular wall mentioned above. From this point there are streaming in, in the dorsomedial direction, a dense mass of cells. These cell-groups cover the flanks of the neuroporic recess.

4. The hippocampal formation, lying in the preceding section on each side of the neuroporic recess, now forms a bridge above the recess, connecting the two hemispheres with each other. The emigrating cell-groups (*h.cm.*) of the preceding paragraph seem to force this bridge in the dorsal direction and to press it together to a relatively thin cell-lamella in the median line. The lamella, together with the emigrating cell-masses, representing a second emigration of hippocampal cell elements, I consider as the hippocampal formation.

5. The zonae limitantes are not very conspicuous.

6. The changes in the subpallial parts are not great. The septal nucleus shows two condensations of cells, a dorsal just below the neuroporic recess and a ventral a little above the medial

border of the tuberculum olfactorium cortex. Between the two ventral nuclei the space is filled up by scattered cells.

7. The bulbar nuclei are confined to the bulbar rudiment. The nucleus olfactorius lateralis is a rather dense cell-mass filling up the space between the bulbar rudiment and the tuberculum olfactorium cortex.

E. Cross-section through the frontal part of the foramen monroi (fig. 15).

In the pallial parts the most striking feature is that the hippocampal formation forms an unpaired medial cell-mass (*h.c.*) and that the thickened medial part (*g.p.t.*) of the general pallium cortex (*g.p.c.*) extends medially to form a little more caudally *a continuous layer above the hippocampal formation* which at the same time decreases to form more caudally a very low cellular ventricular eminence. The cells of the thickened general pallial cortex are not so densely crowded as those of the remainder of the same cortex. Laterally this cortex is confluent with the pyriform cortex (*p.c.*). The zona limitans lateralis (*z.l.l.*) is well pronounced.

In the subpallial parts the ventral septal nucleus mentioned sub C, 6 is found in the medial line between the two cortical layers of the tubercula olfactoria as an unpaired thick ventricular layer of relatively scattered cells. The scattered cells in C, 6 lying between the two nuclei, are found ventral to this unpaired nucleus.

F. Cross-section through the hind part of the forebrain, where the latero-occipital ventricles are disappearing (fig. 16).

In this section the dorsal continuity of the general pallia is broken. The thickened part of the cortex (*g.p.t.*) has grown very greatly and becomes caudally larger and larger so as to fill up the whole dorsal part of the connecting lobe of the telencephalon. The pyriform cortex (*p.c.*) medially is continuous with the general pallial cortex (*g.p.c.*). Laterally it is not well marked from the lateral olfactory nucleus (*n.olf.l.*). Thus a zona limitans lateralis is not to be found in this part of the brain.

The subpallial part has not greatly changed its appearance from the foregoing section. The medial parts of the tuberculum

olfactorium cortex have been replaced by the 'area somatica' of Johnston(?), a cortex-like structure which in the form of a ⌣ covers the brain medially. The band of scattered cells in foregoing sections between the medial extremities of the tubercula olfactoria now is found below the area somatica. In preceding sections there is a more densely aggregated group of cells (*n.t.*) at the medial end of the olfactory cortices. More backwards these condensations are found more lateral and as the ⌣ -shaped area somatica makes its appearance in the series this cell-heap lies below the lateral end of the same area. This cell formation that accompanies and emigrates from the inner part of the tuberculum olfactorium in Cajal preparations has been found to give origin to taenia fibers. It is the nucleus taeniae, hitherto not clearly demonstrated in selachians.

7. Stage of 6.5-cm body length (measured after preservation in formolalcohol). Cross-sections. In this stage no essential changes in the structure of the telencephalon are to be noted. The general arrangement is the same as in the preceding stage, but the different parts are more accentuated than before. Thus the hippocampal rudiment has grown much more distinct with more densely packed cells, especially in its frontal part (fig. 17 A). It now has taken on the aspect of an ordinarily constructed cortical layer. The two hippocampal cortices meet each other above the neuroporic recess.

The medial thickening of the general pallial cortex is greater than before (fig. 17 B) and just at the level of the basis of the processus neuroporicus it joins in the medial line the corresponding part of the opposite side. Here the hippocampal cortex is no longer present.

The pyriform cortex is not distinctly delimited from the general pallial cortex. The zona limitans medialis is absent. The lateral zona sometimes is present, sometimes absent.

The nucleus olfactorius lateralis is more distinct (fig. 17, *n.olf.l.*) than in the preceding stage. Other structures are as before, but somewhat more pronounced.

8. Stage of 8-cm. body length (measured after fixation in 10 per cent formolin). Cross-sections. The definitive arrangement of

the forebrain is attained in principle. The inversion of the pallial parts has become much greater than in the preceding stage. The general pallial thickening has been bent down to a vertical position in the upper part of the 'septum' partly between the hippocampal cortex and the ventricular wall. In the subpallial parts a corresponding process has taken place, and the medial part of the tuberculum olfactorium cortex is also brought to a vertical position. The forward evagination of the forebrain vesicle also is much more pronounced, the 'septum' thus having increased considerably in length. At the foramen monroi, where the 'septum' is broken off, the pallial part of it is separated from the subpallial.

1. Pallial parts. The hippocampal cortex is very clearly seen in the front part of the 'septum,' where it is confluent with the pyriform cortex (fig. 18). The upper end of the hippocampal cortex is bordered by more densely arranged and dark-staining cells (fig. 19, *sub.*). This border or cell-lamina lies inside of the medial part of the general pallium (fig. 19, *g.p.c.*), which is bent down to a vertical situation (fig. 10) in the upper part of the 'septum.' The mentioned border has the appearance of a 'subiculum' as found in reptiles. It begins as soon as the separation of the hippocampal and pyriform cortex has taken place and in front of the general pallium.

The hippocampal cortices are joined with each other by a cellular bridge dorsal to the recessus neuroporicus (figs. 20, 21). This seems to be a result of the secondary medial fusion of the evaginated parts of the forebrain, which had already taken place dorsal and ventral to the tube-like recessus neuroporicus.

The general pallial cortex has grown much thicker than before, the medial swelling being now voluminous and sharply bent down medially in the 'septum' (fig. 1, *g.p.t.*). Towards the foramen monroi, where the general pallial cortices are confluent dorsally (fig. 22, *g.p.c.*), the medial parts are very voluminous, causing at the foramen monroi a thick ridge hanging down from the roof of the ventricle (fig. 22). The main part of the 'episphaerium' of Edinger is made up by the general pallium (figs. 22,

23). The cells here form several dense groups connected with more scattered cell-formations.

The pyriform cortex is in its whole extent tolerably well separated from the general pallium (figs. 19 to 23) and from the lateral olfactory nucleus or the bulbus olfactorius nucleus. Yet fusions of all parts are common, but in such cases the cell arrangement or cell-size makes it always possible to make out the limits of each nucleus. Thus it is always possible to find the situation of the zona limitans lateralis (figs. 19 to 23).

2. Subpallial parts. In the septum the pallial parts are separated from the subpallial by a rather obsolete zona limitans medialis and a sulcus limitans internus. The zona limitans medialis passes immediately dorsal to the neuropore. All parts below this zona belong to the subpallial septum.

The subpallial septum is divided into two parts by a very conspicuous sulcus, accompanied in its hinder part by an ependymal thickening. This 'sulcus septalis' (figs. 21, 22, *s.s.*) begins at the ventral angle of the lateral ventricle. From this it turns obliquely upwards and caudal to the front margin of the foramen monroi, where it is found immediately below the sulcus limitans internus. In the 15-cm. postembryo of Acanthias this sulcus septalis is very sharply pronounced. It marks the ventral limit of the nucleus lateralis septi (fig. 21, *n.l.s.*). At the extreme caudal portion this nucleus sends up a small tongue above the foramen monroi (fig. 22, *n.l.s.*). *This represents a fimbrial structure at least partly homologous with the fimbria in other vertebrates.*

The nucleus medialis septi (figs. 19 to 21, *n.m.s.*) is found as in the preceding stages: in front as a cell-lamina directed upward and forming a dorsal continuation of the cortex tuberculi olfactorii. In the caudal part this lamina is divided into a dorsal and a ventral part, of which the first forms an unpaired cell-mass around the base of the processus neuroporicus. The ventral portion, however, diverges from the dorsal, and at the level of the front part of the foramen monroi it is found in the middle of the basal septum, where it is seen in cross-sections as a rather well-delimited 'nucleus' (fig. 22, *n.m.s.*), lying in the diffusely arranged cell-mass which fills up the basal part of the septum.

The nucleus taeniae (figs. 22, 23, *n.t.*) and the tuberculum olfactorium cortex are not changed in this stage.

The nucleus olfactorius lateralis (*n. olf.l.*) has grown larger and is seen in all sections as a great cellular condensation with somewhat cortical aspect dorsal to the lateral border of the tuberculum olfactorium cortex.

In the lateral wall of the forebrain ventricle there are three 'striatal' swellings, two rostral and a caudal. These represent a striatum. In adult animals these swellings are very strongly developed, containing a ventricular nucleus, described by former writers as 'epistriatum' (figs. 20 to 23, *st.s.*)

9. *Stages of 15-cm. to full-grown animals.* In the further development no essential changes occur. The different parts, excepting the tuberculum olfactorium, however, are growing indistinct. The cortical layers in the pallium lose their characters of well-defined cortices, the cells being spread out and the limits thus being indistinct. This process results in adult animals in a pallium, where it is very difficult to recognize the structures so distinct in the embryo. This condition probably is the reason for the current view, according to which the selachians have no real pallial cortex, except the so-called 'episphaerium' of Edinger. Edinger says (Vorlesungen, 2. Teil, p. 249):

Im caudalen Abschnitte dieses Palliums tritt schon sehr früh, in der ersten Anlage, vielleicht schon bei den Selachiern, sicher bei den Amphibien, eine neue Formation auf, eine Formation, welche keine direkten Riechfasern mehr aufnimmt, wie das Hyposphaerium. Hier münden vielmehr tertiäre Bahnen aus dem Lobus olfactorius. Diesen neuen Abschnitt nennt man Episphaerium. Mit ihm sellt sich zu dem Palaeencephalon das Neencephalon.

Dieses Episphaerium vergrössert sich bei den Reptilien schon so sehr, dass es die Riechnervenendigungen frontaler und lateraler schiebt und zunächst die ganze Medianwand in hinteren Abschnitte und einen Teil der Dorsalwand erfüllt. Immer weiter wachsend erzeugt es dann bei den Reptilien, den Vögeln und namentlich bei den Säugern im wesentlichen das, was als Vorderhirnmasse zunächst auffällt. . . . . Minimal in seinen Anfängen entwickelt es sich aus dem Amphibientypus heraus zu einem immer mächtiger werdenden Organe, an dem schon innerhalb der Reptilienreihe geordnete Rindenbildung vorhanden ist.

This above-quoted view of Edinger coincides by no means with the fact that the forebrain in embryonic selachians contains the main part of structures characteristic of higher vertebrates. Edinger's view thus is morphologically false, based as it is on a false interpretation of the selachian forebrain. Physiologically, Edinger's view perhaps may be right; but the principal reason for his view, the special connections of the 'episphaerium' in selachians, is not established by real observations; on the contrary, there are olfactory fibers of the second order present entering the 'episphaerium.'

Through the results of my observations on Acanthias, the opinion of Lundahl (v. Vetakad:s Handl., Bd. 59. No. 2, 1918), expressed in the most categorical manner, concerning the forebrain phylogeny has no real reason. Lundahl interprets the part of the brain dorsal to the zonae limitantes as a 'palaeopallium.' This view he bases on the suggestion that this part of the forebrain is built up by "numerous, little differentiated nerve-cells," diffusely arranged without forming typical layers. And he finds the statement of this description in papers of v. Kuppfer, Kappers, C. L. Herrick, Edinger, Jakob, and Johnston. That Lundahl's opinion of the pallium in selachians is false follows immediately from the above description of the embryological development of the pallium in Acanthias.

This development also shows the extreme error of the interpretation of the phylogenetic development of the different cortices in the reptilian brain as given by different authors, according to whom the 'palaeopallium,' the 'archipallium,' and the 'neopallium' develop successively from a 'matrix' situated at the fissura rhinalis externa. Such a matrix does not exist in the ontogenetic development. The cortices develop simply from the underlying part of the neuroblastic layer and there are no signs present of a successive displacing of cortical units from a place of origin at the 'fissura rhinalis externa' to more medial situation. All that is true in such a description is that the cortices are developed successively, the pyriform cortex being developed a little before the general pallial cortex; but it is false that all cortices are derivatives from a common matrix, situated as said before. The hippo-

forwards in the shape of a short cornet. This cornet is laterally compressed between the hemispheres. Its opening is very wide (fig. 26), situated just at the level of the foramen monroi. From near the tip of the cornet its dorsal wall is folded into a chorioidal fold (*ch.f.*) hanging down in the cornet and extending backwards in the epithelial roof of the forebrain as the medial chorioidal fold mentioned above. From the form and the height of the recessus neuroporicus it results that the ependymal tela of the forebrain in the pallial region is not fastened at the medial border of the inverted pallium (fig. 28), but some distance dorsal or lateral to this border, a point of attachment peculiar to Chimaera.

In the pallium there are two layers of nerve-cells present, a ventricular and a more distal one. The distal is not very distinct (figs. 24, 25, 27), mostly consisting of scattered cells, sometimes aggregated to form a sort of cell-lamina (fig. 24), sometimes coalescing with the ventricular layer (fig. 26). It is thus impossible to say whether there is really a regular cortical layer present; probably there is one, but studies on embryonic material are necessary for stating this. I have no such material.

The subpallial parts are very strongly developed. The lateral olfactory nucleus (*n.olf.l.*) is very large, covering most of the lateral surface of the forebrain. The lateral brain-wall is very thick and, a little before the level of the foramen monroi, projects a little into the ventricle, forming a swelling which perhaps may be considered as a 'corpus striatum' (*st.s.*). In this swelling is found a condensation of nerve-cells corresponding to the so-called 'epistriatum' in sharks. But this 'epistriatum' is subpallial, and thus not homologous with the 'epistriatum' in reptiles and birds, where it is pallial (hypopallium of Elliot Smith), situated dorsal to the zona limitans lateralis. Farther back from the foramen monroi the lateral wall of the ventricle exhibits another similar swelling (fig. 28, *st.s.2*) of very great distinctness. These two 'striatal' swellings surely are homologous with those of Acanthias. But as they have no special characteristics allying them with the 'striatum' of reptiles, I am not quite disposed to ascribe to them the value of a corpus striatum.[4]

[4] Perhaps, however, they correspond to a real striatum, but there are no special reasons for accepting this view.

In the subpallial region of the forebrain the whole ventral part is covered by a distinct tuberculum olfactorium (*t.olf.*). Behind the pallial portion the tuberculum olfactorium ascends laterally on the brain as far as to the stria medullaris. Caudally, the tuberculum olfactorium ends at the posterior margin of the second 'striatal' swelling ('striatum' of Kappers and Carpenter), where the nucleus preopticus begins.

Dorsal to the medial border of the tuberculum olfactorium lies the medial septal nucleus (figs. 24 to 27, *n.m.s.*). This nucleus never enters the 'septal' portion of the evaginated forebrain. The nucleus lateralis septi is rudimentary. No cellular fimbrial portion of this nucleus is present. A 'sulcus septalis' is present (figs. 25, 26, *s.s.*).

Making exception of some special characters, such as the elongation of the telencephalon medium and the striatal swellings, the chimaeroid forebrain exhibits some conditions which place this type on a lowher phylogenetic stage than the selachian, approaching that of the cyclostomes. Such a primitive character is that the hemispheres are not confluent with each other, but only joined by a chorioidal tela. Also the lack of a nucleated fimbrial portion of the subpallial septum is a primitive character.

DIPNOI

My sectioned material of dipnoan brains being not more than a frontal and a horizontal series of young Protopterus annectens, stained with iron-haematoxylin, I was not able to make any original studies on these animals, beyond the determination of the nuclei. I have found in Protopterus the same conditions as those already found by Elliot Smith in Lepidosiren.[5] I have but

[5] The forebrain of Ceratodus seems to be built up in principle in the same way as in Protopterus and Lepidosiren. In the last number of this Journal that has reached me (vol. 32, no. 1) however, Herrick has pointed out some very great differences between Ceratodus and the other dipnoans; but examining two transverse series of Ceratodus brains I failed to recognize these differences, quoted by Herrick from Bing and Burckhardt ('05). Herrick says: "The lateral outpouching extends but little, if at all, rostrally of the terminal plate and *there is no sagittal fissure separating two cerebral hemispheres behind the olfactory bulbs*. The true (fully evaginated) cerebral hemisphere, accordingly, contains only the olfactory bulb." In my specimens there is a

the fimbrial portion of the septum. This portion, the antero-dorsal, is filled up by more or less scattered cells derived probably from the ventricular wall of the fimbrial portion. These cells represent probably the nucleus lateralis septi. In the postero-ventral part of the septum the medial border of the tuberculum olfactorium is situated. This border is continued dorsad by a lamina of scattered small cell-groups, representing probably a nucleus medialis septi.

The dipnoan forebrain compared with the selachian

At first sight the forebrain of Protopterus seems not to have many features reminding one of that of Acanthias. Nevertheless, a closer examination will reveal dispositions recalling very strongly the selachian conditions. In the subpallial parts the great extension of the tuberculum olfactorium is common to the two groups. Also the extension of the lateral olfactory nucleus, as determined above, seems to be in principle the same, the apparent difference being caused by the greater differentiation in selachians. The septal portion of the subpallium is different, the fimbrial portion being much greater in Protopterus than in selachians. But there is, on the other hand, a great resemblance in conditions. A sulcus septalis occurs in both brains and the fimbrial portion does not accompany the medial border of the hippocampal formation dorsal to the foramen monroi as in higher vertebrates. In selachians, where the hemispheres are joined in the middle line, there is no tela fastened at the posterior margin of the fimbrial portion of the septum as in Protopterus, where the hemispheres are not joined. This tela in Protopterus is probably a part of the lamina (terminalis or) supraneuroporica, which has come to have its attachment at the fimbria owing to a secondary displacement of the nucleus lateralis septi, a displacement which is not difficult to follow in the form-series: Chimaera, Acanthias, Protopterus and Rana.

The pallial parts of the forebrain seem to be most difficult to compare in the dipnoan and the selachian brain. A comparison between the adult Acanthias brain and that of a Protopterus is

impossible to make, but using the brain of a 5-cm. Acanthias embryo, the points of comparison are not difficult to find out. In this embryo the cortex consists of two layers, a distal, where the cells are tangentially stretched, and a ventricular with perpendicular cells. The former corresponds to the cortical layer, the latter to the ventricular in Dipnoi. In selachians also the second layer delaminates from the ventricular position in the embryo, and there is formed a thick cortical plate which wanders up against the brain surface. This cellular mass has before been named 'the general pallial cortex.' To this cortex there is in Protopterus and also in Lepidosiren a corresponding formation in the dorsally greatly thickened cell-layer, bordering the ventricular ependyma dorsal to the ventricle.

Thus there is an agreement in brain structure in Dipnoi and Selachians—an agreement sufficiently great to allow the conclusion that the forebrain types of these groups are to be derived from the same ancestral type with inverted forebrain, with at least ventricular cortex or perhaps with an outer cortex and an inner ventricular cell-sheet. That the last alternative corresponds better with the facts follows from the statement that there are two layers present in Petromyzon. The double cortex, thus, is ancestral in the vertebrate series, and the common ancestors of Dipnoi and Selachii therefore might have had such an one.

THE EVERTED FOREBRAIN IN POLYPTERUS, GANOIDS, AND TELEOSTS

As I have before pointed out, the everted type of forebrain is derived from the inverted, and I have also given some special reasons for this opinion. But I think that no other reason is necessary than the fact that lowlier fish-types, as cyclostomes, selachians, holocephalians, and dipnoans are provided with an inverted forebrain.

As in these primitive fishes the pallium encloses two cell-layers, where a subdivision into three parts at least is indicated, it follows that these conditions may be traceable in the remaining fish-types: crossopterygians, ganoids and teleosts.

The principal characters of the subpallial parts are also the same in selachians, holcephalians, and dipnoans. Thus, these characters necessarily may be present also in the fish-types with everted forebrain, as these fishes belong to the same phylum.

In the following I will try to show that the everted forebrain also in details is built up like the inverted. I begin my description with Polypterus.

Polypterus bichir

The peculiar forebrain of this fish has not yet been described in detail. I therefore will try to make a fuller account of this forebrain.

The telencephalon in Polypterus is evaginated and everted. The evagination is represented chiefly by the ventricles of the bulbi olfactorii (fig. 35). These open into the medial ventricle just at the caudal end of the bulbi (fig. 36), where the foramen monroi thus should be situated. As will be pointed out later, the opening of the bulbar ventricles into the medial ventricle does not perfectly correspond to the foramen monroi in inverted brains.

The eversion of the forebrain is a very peculiar one (figs. 36 to 38). The dorsal part of the lateral wall of the forebrain or the pallium, as it will be named here, is of uniform thickness throughout its whole extent. This pallial lamella has a very great height, but a little above its middle it is bent double to the lateral side, in such a way that its morphological dorsal border points in a ventral direction. Through this eversion the epithelial roof of the forebrain is highly expanded to form a broad tela covering the whole forebrain as in teleosts. Under this everted pallial area lies the very strongly developed subpallial forebrain. The tela is medially strongly infolded, so as to form a longitudinal chorioidal fold (figs. 37, 38).

The pallium. Above I have called the everted portion of the forebrain vesicle the pallium. This requires a further explanation. I have before defined the pallium as being a brain part lying dorsal to the zonae limitantes and practically also dorsal to the sulci limitantes. As has been pointed out by Johnston, the bulbar

ventricle is continued into the lateral wall of the brain as the sulcus limitans externus, dorsal to which the pallium is situated. In Polyterus the bulbar ventricle also is continued backwards in the brain wall by a short sulcus (figs. 37, 38). This sulcus must be the sulcus limitans externus. Thus the brain parts dorsal to this sulcus may contain the pallium. Dorsal to the sulcus there follows in the rostral part of the forebrain in Polypterus a short ventricular band devoid of nerve cells (fig. 37, 38) covered by a simple thin layer of ependymal cells. Lateral to this band the brain wall is nearly without cells. In this way a distinct limit between the relatively cell-rich subpallial and cell-poor pallial parts is formed. This limit has not, except in the medial part, the character of a regular zona limitans (*z. l. l.*), owing to the fact that the cells in the pallium are situated at the ventricle, leaving the rest of it almost devoid of cells.

More caudally, where the sulcus limitans externus disappears, the cell-free ventricular space is filled up by small cells, and thus the ventricular part of the zona limitans also disappears. But here begins a deep sulcus, *a sulcus limitans pallii lateralis* (figs. 37 38, *s.l.p.*), marking the ventral limit of the pallium.[8] It lies exactly at the limit between the pallium and the subpallial parts and passes along the side of the forebrain almost to its caudal end. To some degree this sulcus depends upon the direction of the basal portion of the pallium, which is more or less inclined against the medial line. As in the caudal end of the forebrain the pallium becomes vertical, the sulcus becomes less pronounced.

In the pallium of Polypterus nerve cells are present in two different situations. The main part forms a relatively thick ventricular layer (figs. 35 to 38), the others are sparsely distributed in the dense neuropil mass of the pallium. Thus there are two pallial layers as in all hitherto described forms. The ventricular layer is subdivided into three parts (figs. 37, 38), a medial (*p.c.*), a dorsal (*g.p.c.*), and a lateral (*h.c.*). The medial part of the layer

[8] In Amia Johnston has named this sulcus the 'sulcus limitans hippocampi.' In higher animals the 'sulcus limitans hippocampi' belongs to the medial wall of the inverted brain. *It is not homologous to the ganoid one.* Therefore, I have changed its name in Polypterus.

The above description is based upon a transverse series of sections through an adult Polypterus forebrain. But I have also studied the forebrain of younger stages. Through the kindness of Professor Jägerskiöld (Gothenbourg), I had the opportunity of investigating two stages, one (with retained outer gills) of 4.5 cm. total length and the other of 12.5-cm. These stages exhibit in principle the same morphological arrangement in the forebrain as the adult. In the 4.5-cm. stage the lateral olfactory nucleus is under formation from the pars superior of the precommissural body, as suggested in the adult. The eversion of the pallium is in principle the same as in the adult, but the bending of the upper portion of the pallium is in the youngest stage by far not so advanced as in the 12.5-cm. stage and in this it is much less advanced than in the adult. Of very great phylogenetic interest is the fact that the descending part of the pallium is much greater in the adult than in the 12.5-cm. stage and that in the 4.5-cm. stage one can scarcely speak of a descending portion, the pallium being composed of a high ascending part and a bent-out portion of smaller size. In the larger stages the brain-case is very spacious dorsoventrally and there is a rather wide free space between the roof of the brain case and the pallium. In the 4.5-cm. stage, however, the pallium lies in the closest contact with the roof of the skull and the relations between skull and forebrain are such as to make it evident that the bending out of the pallium is caused by lack of space for the outgrowing of the pallium in the dorsal direction. This stage of 4.5-cm. makes it very probable that it has been preceded by a stage where the pallium was uneverted, directed straight dorsad or perhaps bent in a little. The latter presumption is based on the fact that the pallium at the line of attachment of the tela makes a little bending in opposite direction to the general bending of the pallium. Thus, I find it very probable that in younger Polypterus stages there is even a somewhat inverted forebrain present. This being the case, the forebrain of Polypterus may serve very well for connecting the everted forebrain type with the inverted as present in dipnoi or holocephalians. The chief difference is the lack of forward evagination in Polypterus, but in Chimaera this evagination is very small, as pointed out before.

Ganoids and teleosts

In Polypterus all structures characteristic of all other fishes are present. In ganoids and teleosts these structures are repeated, but somewhat modified. Thus it is not necessary to describe minutely the brain of those fishes. I can restrict myself to the most striking differences.

In all ganoids the pallium is not of uniform thickness throughout, as in Polypterus, and thus the outer surface is not parallel with the ventricular. In Acipenser the ventricular surface is transversely rather convex, but the outer surface is flat. Thus, in a transverse section the distance between the zona limitans and the point of attachment of the tela is much longer than the distance between the latter point and the fovea externa. In other ganoids this difference in length is much greater, as the pallium is much thicker in the middle than in Acipenser, and in teleosts the tela is attached close to the fovea externa.

Thus, in actinopterygians (ganoids and teleosts) the development seems to go from a moderately thickened pallium to an extremely thickened one; that is, from a pallium with relatively long lateral outline to one with very short.

In all actinopterygians the pallial cells are grouped in three more or less well-limited parts, corresponding to the three parts in Polypterus. But in all actinopterygians the pallial cells have wandered in from the ventricular sheet to a greater extent than in Polypterus. In Acipenser, Scaphirhynchus, and Polyodon the cortical cells form cell-laminae with cortical arrangement throughout the whole pallium, with but few cells in the ventricular position. In a young Lepidosteus (fig. 39) a ventricular layer covers the whole ventricular surface, but the main part of the pallial cells has wandered in.

In teleosts the three pallial parts are very well limited, but the cortical arrangement of cells is not always well pronounced. In Osmerus I have described this arrangement (see my paper in Acta Zoologica, vol. 1, 1920).

The zona limitans is very conspicuous in Lepidosteus (fig. 39, *z.l.l.*) and Amia (Johnston) and in many bony fishes, but in

Acipenser, Scaphirhynchus, and Polyodon the zona is only to be seen in the foremost part of the forebrain. There is, however, no difficulty in making out the limit between the pallial and subpallial parts, owing to very pronounced structural differences between these parts, the pallial neuropil being denser than the subpallial.

A sulcus limitans pallii lateralis generally is not present in ganoids and teleosts, except in Amia, where Johnston has found such a sulcus, and in Acipenser, where it is present in the foremost part of the forebrain.

The subpallial parts in ganoids in principle are built up as in Polypterus. In Lepidosteus, Amia, and teleosts a very well-defined nucleus olfactorius lateralis below the zona limitans is present. In Lepidosteus (and Amia) this nucelus is very interesting, being formed by cells grouped together in islets or clusters, very well differentiated in the preparations from all other cells in the subpallial parts. Thus, it is here possible to make out the limits of this nucleus more fully than in other fishes. The nucleus olfactorius lateralis is composed of a lateral part, forming a cell-lamina in the lateral portion of the brain-wall (fig. 39, *n.olf.l.*). From this lamina a process extends medially to join the ventricular ependymal layer just below the zona limitans, dorsal to the precommissural body (*p.p.s.*). Through this process the ventricular situation of the nucleus olfactorius lateralis is clearly demonstrated in Leipidosteus. Johnston has shown that the nucleus olfactorius lateralis in Amia is built up almost in the same way. The opening of the bulbar ventricle is caudally continued by a groove of different shape and length in different fishes. In Acipenser this groove is not very pronounced, forming a shallow concavity in the foremost part of the forebrain. In Lepidosteus the groove is very broad, rostrally forming a semicircular excavation (fig. 39, *s.l.l.*) in the ventricular wall. Caudally, near the commissural bed, the excavation becomes shallower and disappears. The ependymal layer, covering the excavation, is thick. In Amia (Johnston) the sulcus is a narrow ependymal groove. In Osmerus (teleost) the rostral part is a relatively broad excavation, as in Lepidosteus. Caudally this excavation becomes

narrower and disappears, leaving an ependymal thickening as witness to its earlier existence also in the caudal region of the forebrain.

In all fishes the precommissural body is divided into an upper and a lower portion: pars superior and pars inferior. A nucleus olfactorius anterior pars precommissuralis I have found in Osmerus in the same position as in Polypterus, but extending further backwards. In ganoids I have found no such nucleus, owing probably to the preservation of my material. In Polypterus, as in all ganoids and teleosts, the preoptic nucleus is composed of a magnocellular and a parvocellular part. Also a pars recessi is present. The recessus preopticus is very broad in ganoids, narrower in teleosts.

The nucleus taeniae (entopenduculаris) in ganoids and teleosts, as in Polypterus, is penetrated by the lateral forebrain bundle.

Summary of the forebrain in Polypterus, ganoids, and teleosts

The forebrain in all fishes is built up according to a common scheme, but Polypterus, in the character of the eversion of the pallium and in the broad medial ventricle, occupies a separate place. The shape of the pallium should perhaps be taken as argument for an idea of a special eversion process, independent of that in other fishes. The fact, however, that the subpallial parts do not differ from those in other fishes seems to overthrow such a theory. Thus, I think that the everted forebrain in Polypterus is to be derived from the same source as that in other fishes with everted forebrain. Polypterus, thus, in this respect belongs more to the actinopterygian stem than to the crossopterygean-dipnoan.

The scheme of forebrain construction in all fishes with everted forebrain thus may be that of the diagram, figure 40. In this diagram all nuclei are brought back to the probable position of their matrix formations at the ventricular wall. Beginning from the dorsal border of the pallium and following the inside of the ventricle ventrad, we meet the following structures:

I. Pallial parts.
  a. Hippocampal pallium (*h.p.*).
  b. General pallium (*g.p.*).
  c. Pyriform pallium (*p.p.*).
II. Zona limitans (lateralis) (*z.l.l.*) and sulcus limitans pallii lateralis (*s.l.p.l.*).
III. Subpallial parts.
  d. Nucleus olfactorius lateralis (*n.olf.l.*) and sulcus limitans lateralis (*s.l.l.*).
  e. Corpus precommissurale, pars superior (*p.p.s.*).
  f. Nucleus olfactorius anterior pars precommissuralis (*p.n.o.a.*).
  g. Nucleus entopeduncularis, or taeniae (*n.t.*).
  h. Corpus precommissurale pars inferior (*p.p.i.*) and, in the caudal part of the forebrain, nucleus preopticus.

COMPARISON BETWEEN THE EVERTED AND THE INVERTED FOREBRAIN IN LOWER VERTEBRATES

A diagram of the inverted forebrain made up in the same way as that of the everted shows the following structures (fig. 41):

I. Pallial parts.
  a. Hippocampal pallium (*h.p.*).
  b. General pallium (*g.p.*).
  c. Pyriform pallium (*p.p.*).
II. Zona limitans (*z.l.*)
III. Subpallial parts.
  d. Nucleus olfactorius lateralis (*n.olf.l.*) and sulcus limitans lateralis (*s.l.l.*).
  e. Tuberculum olfactorium (*t.olf.*).
  f. Nucleus medialis septi (*n.m.s.*).
  g. Nucleus entopeduncularis, or taeniae (Dipnoi) (*n.t.*).
  h. Nucleus lateralis septi (*n.l.s.*) and, in the caudal part of the forebrain, nucleus preopticus.

The idea of the comparative anatomy of the everted forebrain recently has undergone a very important change, especially through the excellent works of Johnston. This author is of the opinion that the so-called 'striatum' of earlier authors belongs to the pallium. He names this part, situated dorsal to the zona limitans, the primordium hippocampi. In this part Kappers and Sheldon have found three different parts, separated in teleosts by well-marked sulci. These parts, however, have been differently interpreted. Kappers supposes that they represent a lateral palaeopallium, a dorsal striatum, and a medial

epistriatum—a conception which does not coincide with the fact that this epistriatum is situated morphologically ventral to his striatum. Sheldon is of the opinion that the three parts are: a medial primordium hippocampi, a lateral nucleus olfactorius lateralis with a pyriform lobe, and a centrally situated palaeostriatum. This opinion is contradicted by the fact that his primordium hippocampi is morphologically ventral to his nucleus olfactorius lateralis and to his pyriform lobe.

In my paper on the forebrain and 'tweenbrain of teleosts I have adopted another terminology. The primordium hippocampi of Johnston I have named 'primordium pallii.' Now I will change this name to 'pallium' only, as being more consistent with the conditions in lower vertebrates. This pallium corresponds fully with the pallium in inverted and evaginated brains as being a part of the brain situated dorsal to the zona limitans and the sulcus limitans externus. This pallium is subdivided into three parts, corresponding to the parts named by Kappers in another way. I have called them, respectively, the primordium hippocampi, the general pallium, and the pyriform lobe, and this nomenclature seems to me to be a consequence of my idea of the pallium in teleosts. In inverted brains the most dorsal (=medial) part of the pallium is the hippocampal pallium, the middle (=dorsolateral) part the general pallium, and the ventral (=lateral) part the lobus pyriformis. Under the supposition that the subdivision of the pallium is the same in all lower vertebrates, the homology must be well settled. This supposition is no arbitrary one, but is supported by the fact that it is present already in selachians and Polypterus, that is, in more primitive forms than ganoids and teleosts. Thus, I think, there is no serious objection to make against the homology of the pallial parts. It is clear, however, that the homology is not perfectly proved until it is shown that the fiber connections do not speak decidedly against the homology. But it is still too early to draw the fiber connections into the discussion, these being too little known in selachians and holocephalians and practically unknown in Dipnoi and Polypterus. But so far as known to-day, the fiber connections do not speak against the homology.

In the subpallial parts the nucleus olfactorius lateralis in all brains, everted as well as inverted, occupies the same position in the lateral part of the brain-wall at the sulcus limitans externus, just ventral to the zona limitans, and the conditions especially in Lepidosteus make the homology of that nucleus very probable. Also the fact that a part of the lateral olfactory tract splits up in this nucleus both in inverted and everted brains is of the nature to settle the homology.

In the inverted brain the tuberculum olfactorium is formed from the neuroblastic layer ventral to the nucleus olfactorius lateralis or the sulcus limitans lateralis (externus). In the everted forebrain the superior part of the nucleus precommissuralis occupies the corresponding part of the ventral wall, and therefore must be homologous with the tuberculum olfactorium. That there must be a homologue of the tuberculum olfactorium present in ganoids and teleosts follows from the fact that this part of the brain is present in selachians, holocephalians, Dipnoi and tetrapods, and in ganoids and teleosts there is no other part to be found with corresponding position. The difference between the true tuberculum olfactorium and that of ganoids and teleosts is that in the latter groups the cells do not form a cortical layer as in the former, but keep their original place at the ventricular wall. It is, however, possible that the ventricular position is secondary in ganoids and teleosts, as well as in Dipnoi and Amphibia!

Ventral to the corpus precommissurale pars superior in ganoids and teleosts comes the pars inferior of the same corpus. This nucleus is ventricular and forms the ventral part of the brain-wall rostral to the commissural bed. Its morphological position is the same as that of the nucleus lateralis septi of the inverted brain, since it must be borne in mind that the subpallial septum is the medial ventral part of the forebrain ventricle which is brought into its septal position through the evagination of the hemispheres. Thus the morphological situation of the pars inferior of the precommissural body is that of the nucleus lateralis septi in the inverted forebrain.

As to the homology of the nucleus medialis septi in the inverted and nucleus olfactorius anterior pars precommissuralis in the everted forebrain, some facts seem to support this view:

1. In Polypterus, where there is a small septum present, the nucleus olfactorius anterior (= lobus olfactorius) sends a process (pars precommissuralis) into this septal structure.

2. In Acanthias, where in front the nucleus olfactorius lateralis occupies the ventral part of the frontal surface of the hemispheres, it sends a cell-lamina into the subpallial septum. This cell-lamina is the nucleus medialis septi.

3. In the embryo of Rana (according to investigations made at this institute by Miss G. Söderberg) the granule cell-zone in front of the hemispheres is continued into the septum by the nucleus medialis septi.

The nucleus taeniae, or entopeduncularis, in teleosts is probably a derivation from the nucleus precommissuralis pars superior. Certain observations in the ontogeny of Salmo (made at this institute by G. Lindén) have shown its derivation from the portion of the ventricular wall occupied later by the superior part of the precommissural body. In Dipnoi, where a nucleus taeniae is also present, it is associated with the tuberculum olfactorium. As well in ganoids and teleosts as in Dipnoi, it is penetrated by the lateral forebrain bundle. I think there may be no serious objection to be made against this homology.

Hitherto, I have thought, like Johnston, that the nucleus taeniae is a homologue of the 'somatic area' in selachians. This view I do not now find well grounded, as my investigations on the selachian brain seem to have shown that the 'somatic area' in selachians is part of an unusually large nucleus preopticus.

After the above discussion I venture to make up the following scheme of the forebrain homologies in lower vertebrates:

the brain in the living descendants, it seems possible to get a rough idea of this subject, especially if the phylogenetic relations of the extinct groups are used for guidance.

From the crossopterygians the Dipnoi, the polypterids, and the actinopterygians are generally derived. Of the crossopterygian descendants, the Dipnoi have an inverted forebrain, the polypterids and actinopterygians an everted. Assuming that the descent of these three groups of fishes is rightly interpreted by paleontologists, the eversion took place in the crossopterygian group or in nearly allied descendant groups. The crossopterygians are found from the lower Devonian to the upper Cretaceous. But the actinopterygians began also in the Devonian with crossopterygian-like fishes, as the palaeoniscids and others. Thus the eversion of the forebrain may have taken place very early, probably already in Devonian fishes, or perhaps earlier.[7]

From primitive crossopterygians the Dipnoi undoubtedly are descendants. The earliest Dipnoi are found in the Devonian. In the living species the forebrain is inverted. Thus it seems to be probable that the inverted forebrain, as being the primitive type of vertebrate forebrain, also was the brain type in primitive crossopterygians of the Devonian. As in all recent descendants of the crossopterygian group and also in the plagiostomes the pallium contains two cell-layers, a cortical and a ventricular, this must also have been the case in the crossopterygians. Further, it is probable that the pallium was already subdivided into the typical three parts, the hippocampal, the general, and the pyriform pallium. This is a conclusion drawn from the fact that in Polypterus, ganoids and teleosts the subdivided pallium is the rule. But also in Dipnoi there are signs of a subdivided pallium. Also in the parallel group of selachians a similar subdivision is present, at least in the embryo. The eversion of the forebrain in Polypterus and ganoids must have taken its origin from a slightly

[7] Judging from the shape of the skull and the position of the optic and trochlearis foramen in the newly described crossopterygian genus Wimania from the Triassic, the forebrain ought to have been very elongate and laterally compressed as in dipnoans and Polypterus. In the triassic palaeoniscid Birgeria the brain-case is much shorter, laterally compressed and rapidly narrowed in front, suggesting a forebrain of the same type as in the young Lepidosteus.

inverted forebrain, where the medial portions were not joined in the mid-line. Such a forebrain is present in the recent Dipnoi. Thus it seems very probable that also in primitive crossopterygians such an inversion was present. This assumption is supported by the fact that in the holocephalians and in petromyzonts this brain type is the rule.

In the ependymal roof of the forebrain there is in ganoids and teleosts and also in Dipnoi and holocephalians a medial infolding in front of the paraphysis. This medial fold might have been present also in the primitive crossopterygians. (In holocephalians this fold begins at the top of the recessus neuroporicus.) A paraphysis was also probably present.

The hemispheres were in primitive crossopterygians probably moderately evaginated. This is an assumption based upon the fact that in Polypterus, ganoids, and teleosts the evagination is confined to the foremost part of the forebrain, the bulbus olfactorius, and in holocephalians also is not very pronounced. Against this assumption is the fact that in recent Dipnoi the hemispheres are excessively evaginated. But here the evagination is of a quite peculiar nature, being confined to a great extent to subpallial brain parts. The evagination, corresponding to that in ganoids, that is, the evagination that ends in the bulbus, is not greater, however, than in holocephalians. In recent Dipnoi (except in Ceratodus) the bulbar ventricle is rudimentary. As a special bulbar ventricle is absent in holocephalians, present in Polypterus and ganoids and also in selachians and petromyzonts, it seems probable that also in primitive crossopterygians there was a bulbar ventricle, at least of moderate size.

In all vertebrates with inverted and evaginated forebrain a zona and a sulcus limitans medialis (except in cyclostomes) and a sulcus limitans externus occur. These structures might have also been present in primitive crossopterygians. As the occurrence of a zona limitans lateralis is variable in vertebrates, it is not possible to determine whether such a zona was present in the crossopterygians.

In the subpallial parts, the ventricular position of the nuclei in Dipnoi seems to indicate that the same was the case in the

PLATE 1

EXPLANATION OF FIGURES

1 Ammocoetes, 1 5 cm. Transverse section through the posterior part of the forebrain.

2 Ammocoetes, 3 cm. Transverse section through the opening of the caudal ventricular diverticulum.

3, A, B Transverse sections, A, through the 'primordium hippocampi' of Petromyzon, B, through the 'eminentia thalami' of Triton.

4 Ammocoetes, 3 cm. Transverse section through the opening of the olfactory ventricle.

5 Acanthias, 3 3 cm. Transverse section through the foramen monroi.

6 Acanthias, 3 3 cm. Transverse section through the middle of the forebrain. Same series as figure 5.

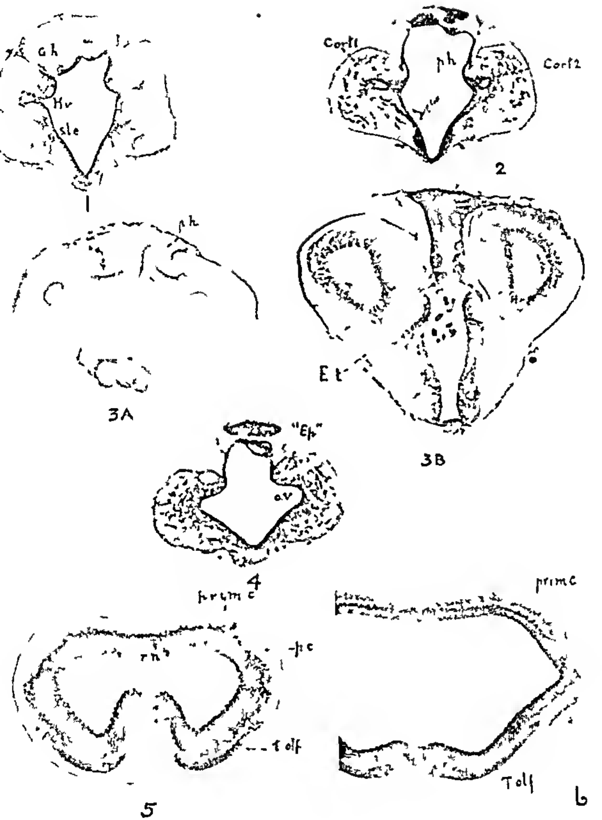
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PLATE 2

EXPLANATION OF FIGURES

7 Acanthias 3 7 cm. Transverse section, passing through the bulbus olfactorius.

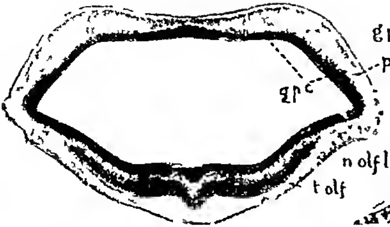
8 Acanthias, 3 7 cm. Transverse section through the lateral part of the pallium.

9 Acanthias, 4 cm. Transverse section taken before the foramen monroi.

10 Acanthias, 4 cm. Transverse section a little behind the front part of the foramen monroi.

11 Acanthias, 5 cm. Transverse section taken through the rostral part of the hemispheres.

12 Acanthias, 5 cm. Transverse section taken somewhat behind the section figured in figure 11.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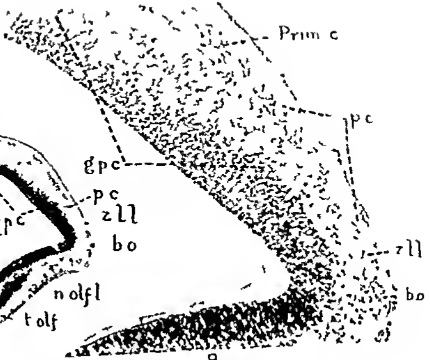
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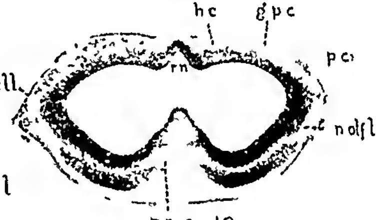
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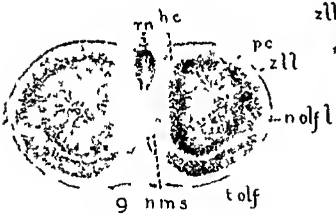
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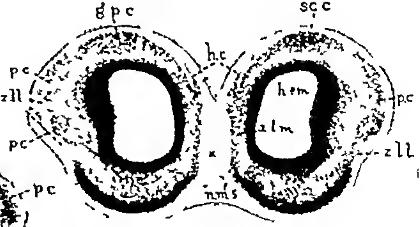
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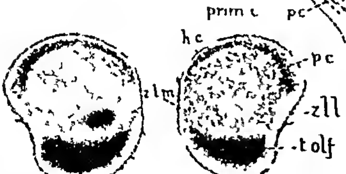
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PLATE 6

EXPLANATION OF FIGURES

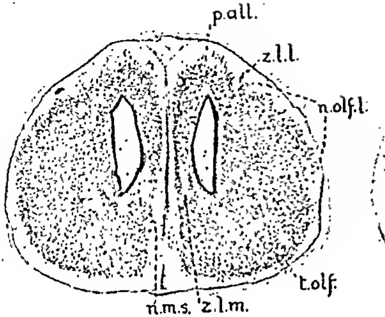
24 Chimaera. Transverse section through the evaginated part of the forebrain.

25 Chimaera. Section taken somewhat behind figure 24. Same series.

26 Chimaera. Section taken just in front of the foramen monroi. Same series.

27 Chimaera. Section taken a little behind figure 26. Same series.

28 Chimaera. Section through the posterior portion of the pallium. Same series.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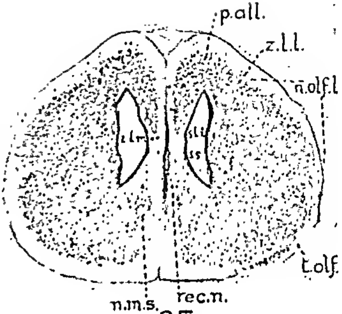
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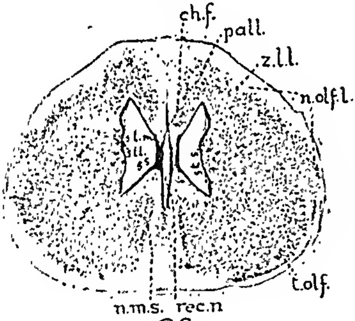
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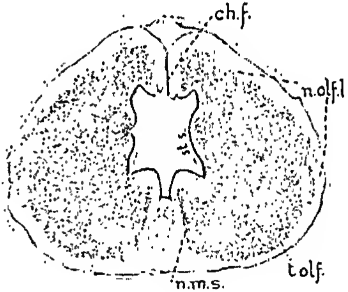
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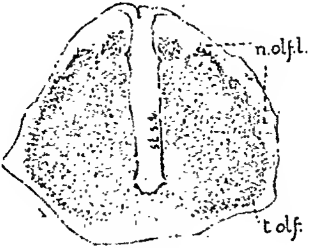
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28

PLATE 7

EXPLANATION OF FIGURES

29 Protopterus. Transverse section taken through the rostral part of the pallium.

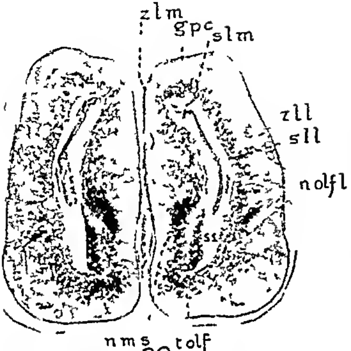
30 Protopterus. Section taken somewhat behind figure 29. Same series.

31 Protopterus. Section taken somewhat behind figure 30. Same series.

32 Protopterus. Section taken somewhat behind figure 31. Same series.

33 Protopterus. Section taken just in front of the foramen monroi. Same series.

34 Protopterus. Section taken through the foramen monroi. Same series.



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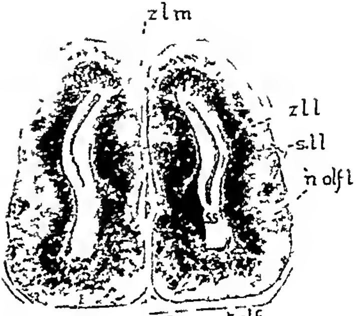

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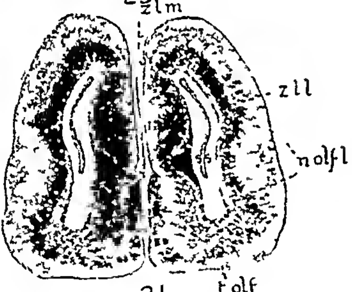

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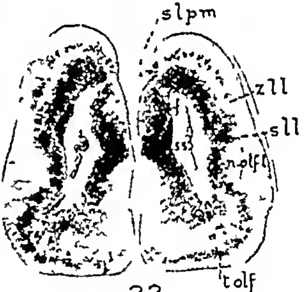

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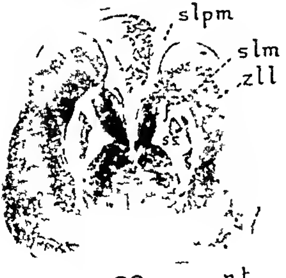

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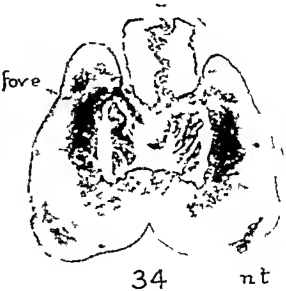

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tures should be when first laid down coextensive. Since I have shown that a differentiated floor plate extends no farther forward than the fovea isthmi, the primary extent of the notochord would thus fall far short of the point marked out as its anterior end by His, namely, the point where sutura terminalis, sutura neurochordalis, ectoderm, and entoderm (i.e., pharyngeal membrane) adjoin (cf. the His fig. 1, 1892, 2 paper, reproduced in my earlier paper as figure 4).

The question as to whether or not it is permissible to recognize a primitive suture, actual or potential, uniting the right and left halves in the epichordal portion of the body is a purely embryological one and it is not proposed to enter into its discussion here. More pertinent at this time is the determination as to whether or not floor plate and notochordal plate are primarily coextensive, and hence whether, granting the propriety of the term suture, it may likewise be designated as neurochordal suture. This determination is somewhat difficult for two main reasons: 1) At the early developmental stage in which notochord and neural plate are in juxtaposition the floor plate is still undifferentiated. Likewise in most forms at least the anterior end of the notochord is not at first clearly demarcated from the prechordal plate (preaxial mesoderm). 2) The neural plate (tube) and notochord grow markedly and at different rates, the former obviously more rapidly, so that the neural tube becomes bent away and separated from the notochord so that by the time the fovea isthmi is evident and the floor plate distinguishable through its differential change, the points for comparison are quite remote from each other. These difficulties do not, however, render valueless a comparison of neural plate and notochordal plate and recourse may again be had to the median plane relations in progressively older stages.

Shark. Sixteen median plane reconstructions were made of shark embryos from 1.5 to 23 mm. length, of which ten are reproduced as plate 2. The magnification is the same for all so as to permit more readily visualization of the growth changes. Figures 17, 19, and 20 are from the embryos shown in figures 6, 11, and 13, respectively. Figures 18, 21, and 22 are of stages

intermediate to those of 9 and 10, 13 and 14, and 15 and 16, respectively. Figures 23 to 26 are of progressively older stages, all of them, however, older than that represented by figure 16.

While in figure 17 the notochord is included in the entoderm and its prospective cephalic end is indeterminate without a comparison with the mesoderm and with later stages, in the succeeding stages figured it is separated off save at its cephalic and caudal ends where prechordal plate and marginal zone (blastoporic lip) are united to it. Both of these zones mark regions where notochord, paraxial mesoderm and entoderm are confluent. In the case of the marginal zone, of course, the neural plate must be added to these. The prechordal plate is a region of great significance in understanding the morphology of the head. Without stopping to consider the neural plate-notochordal plate relations more closely at this point, it is obvious at once from a survey of these figures that not only does the anterior end of the notochord fail to reach the anterior end of the neural plate, but falls far short of the primitive infundibular fold, being separated from it by the greater extent of the prechordal plate (cf. figs. 17 to 20) in which it ends.

Turning to a more exact comparison of notochord and neural plate, in order to determine if possible the point in the neural plate with which the anterior end of the notochord primitively corresponds, it should be noted that only in the last figure of the series (fig. 26) is the fovea isthmi and the cephalic end of a differentiated floor plate distinguishable, where it has been designated by the letter *I*. The interval of the medial stretch of floor between this point and the tuberculum posterius of von Kupffer is in the shark embryo of this stage extensive. *P* marks the latter landmark. No significant alterations in form development take place between this stage and the 40-mm embryo figured in my earlier paper (figs. 1 and 8), with which it may be compared. Each preceding earlier stage has been compared and the equivalent point similarly designated, back to and including that of figure 19. In this comparison the descriptions and figures of Neal ('98), von Kupffer ('06), and Scammon ('11) have been considered and compared, particularly the time plates

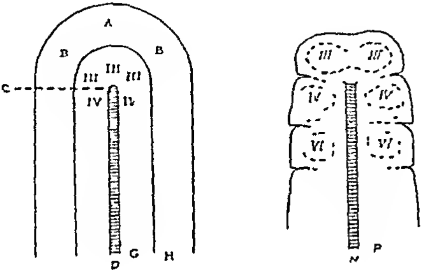
of the figures of plates 2 and 3. The important relations of notochord and prechordal plate are more adequately discussed by Adelmann ('22).

CONCLUSIONS

In the foregoing pages the four interpretations outlined in the introductory paragraphs of this paper have been examined from the three points of view proposed on the question of fact, and the conclusion is safe, I think, that the His interpretation and that of Schulte and Tilney fail to satisfy the requirements. Johnston's observations have been confirmed in the essential feature that the neural plate terminates with the chiasmatic ridge and that the primitive infundibular furrow is likewise a primitive optic furrow. My own interpretation has added what I regard as an important point—the recognition of a primitive continuity of nervous parietes in the brain anterior to (cephalad of) the notochordal axis, together with a more correct evaluation and limitation of the sutura neurochordalis of His. It is felt that there has been given an interpretation also consistent with the actual facts of brain growth and with the pattern of vertebrate ontogeny which was less apparent if the approach was from the neurological side as in the case of the researches of Johnston and Schulte and Tilney. As has been insisted earlier in this paper, the developmental origin of the brain plate and the morphogenesis of the brain are primarily embryological questions inseparable from the pattern of morphogenesis of the head and of the body as a whole.

It is not my intention to consider in any detail the embryologic aspects of the problem in this place; it is, however, advantageous to briefly mention some contributory evidence from the embryological side. Stated succinctly, it is clear that the vertebrate brain arises from the dorsal blastoporic lip which by growth effecting essentially a potential closure of the blastopore, produces an arrangement of material in the neural plate illustrated in figure 2, D, in which the neurochordal suture marks such a line of 'closure,' while the floor plate is a differentiation along this line expressing the primitively bilateral character of the growth of nervous material. Beneath the neural plate the mesoderm and

notochord exhibit a similar arrangement. For a more adequate comparison on this important point figure 6 of my previous paper is here reproduced as figure 5 A while figure 5 B reproduces the plan of arrangement of notochord, preaxial and paraxial



5 A 5 B

Fig 5 Schemas comparing the cephalic portion of the neural plate with the underlying notochord-mesoderm relations

5 A (Copied from Kingsbury, '20, fig 6) Diagram to illustrate the interpretation of the cephalic portion of the neural plate *A*, region of the retinal area (s) *B*, the region of the olfactory lobes (and cerebrum), *C*, cephalic end of the floor plate (and sutura neurochordalis), *D*, the floor plate, *G*, primary motor zone, *H*, primary sensory zone, *III*, nucleus of oculomotor nerve, *IV*, nucleus of trochlearis nerve

5 B Portrayal of the relations of notochord and mesoderm as they exist in a form in which the head cavities are well developed *III*, premandibular somites and cavities with their prechordal connection and cross canal, *IV*, mandibular somites and cavities, *VI* Hyoid somites and cavities The lateral mesoderm and pericardial cavity are of course related but not indicated

mesoderm essentially as it would exist in any form (e g, shark, turtle, certain birds) in which the 'head somites' are well developed. To make the comparison more forceful, the cranial nerve number marks the somite from which its territory of innervation is derived.

It is not the purpose of this paper to consider the question, in how far this conception of the brain plate may assist in the understanding of the purely neurologic problem of the structural pattern of the brain, but there is much that is suggestive. The floor of the midbrain, the ganglion interpedunculare, the corpus mammillare particularly, invite examination, while many fundamental structural relations of the vertebrate brain might be mentioned whose review from the standpoint here presented would be indicated. Inasmuch as other aspects of the broad problem of developmental pattern claim the writer's attention, he does not plan, for the present at least, to test further the neurological possibilities of the interpretation, even though a strong curiosity in the matter prompts thereto. It is hoped, however, that the concept may afford a sound basis for neurological investigation.

In closing, I wish to acknowledge the kindness of Prof. S. H. Gage who placed at my disposal the chick and shark embryos[6] of the collection in his charge, and the helpful coöperation of Mr. H. B. Adelmann at points where my line of investigation crossed with his.

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[6] Many of these series bear evidence of the attention Mrs. S. P. Gage had devoted to the problem of the anterior end of the neural plate. That she had definitely rejected as not satisfactory the His plan of arrangement of the zones is apparent from her paper of 1905. Doubtless had her health been spared she would have arrived at some alternative explanation, such as that here presented.

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PLATE 1

EXPLANATION OF FIGURES

Photographs, all at a magnification of ten diameters, except figure 16 which is × 8. Embryos of Squalus acanthias dorsal aspect.

6 Series 42, no somites, length 1.5 mm.
7 Series 45, 6 to 7 somites, length 2.2 mm.
8 Series not sectioned, length 2.4 mm.
9 Series 48, ca. 8 somites, length 2.16 mm.
10 Series not sectioned, length 2.18 mm.
11 Series 52, 11 to 12 somites, length 2.9 mm.
12 Series 54, 13 to 14 somites, length 3.5 mm.
13 Series 55, 15 somites length, 4.0 mm.
14 Series 59, ca. 17 somites, length 4.8 mm.
15 Series 69, 29 somites, length 5.0+ mm.
16 Series 75, 41 somites, length ca. 7.0 mm.

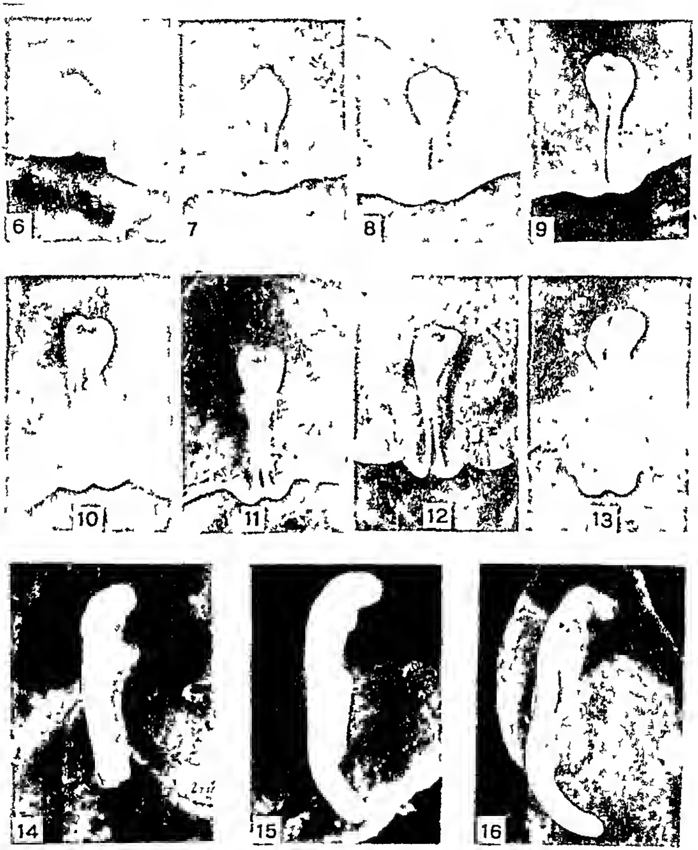


PLATE 3

EXPLANATION OF FIGURES

Median plane reconstructions from sagittal sections of the chick embryo, head region only. The notochord is indicated by cross-barring, the neural plate stippled, entoderm and preaxial mesoderm (prechordal plate) stippled; the ectoderm shown in black. All figures at the same magnification, × 50.

27 Series 139, 6–7 somites.

28 Series 106, 10 somites.

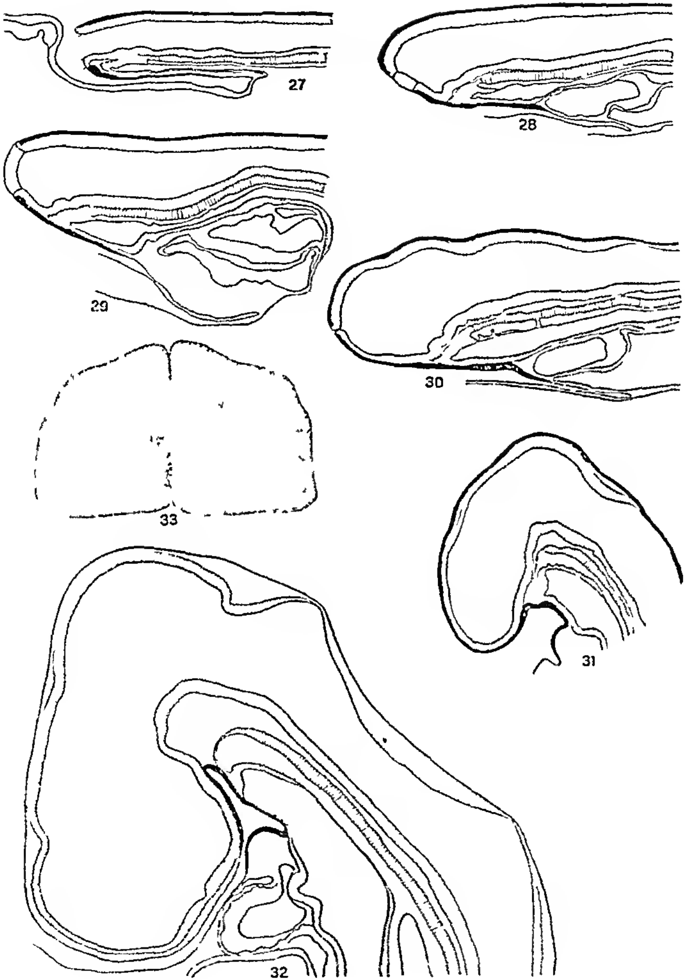
29 Series 119, 14 somites.

30 Series 109, 16 somites.

31 Series 127, 22 somites.

32 Series Gage 54s, 30 + somites.

33 Ventral view of a model of the head of a chick, eight to nine somites, anterior portion, × 67. To illustrate the ventral end of the 'sutura terminalis' marking the anterior end of the brain-plate. Back of it is the 'hypophyseal area' and a shallow Seessel's pocket continuous caudally with a dorsal pharyngeal groove.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Abstracted by Ottorino Rossi, author
University of Sassari, Italy.

On the afferent paths of the sympathetic nervous system, with special reference to nerve cells of spinal ganglia sending their peripheral processes into the rami communicantes.

In embryos of birds (sparrow) and mammals (pig) there is demonstrated for the first time by direct anatomical observation the occurrence in the spinal ganglia of nerve cells, the peripheral processes of which pass into the rami communicantes. These are the cells of origin of Kölliker's fibers and are regarded as afferent visceral sensory neurons.

AUTHOR'S ABSTRACT OF THIS PAPER ISSUED
BY THE BIBLIOGRAPHIC SERVICE JULY 24

ON THE AFFERENT PATHS OF THE SYMPATHETIC NERVOUS SYSTEM, WITH SPECIAL REFERENCE TO NERVE CELLS OF SPINAL GANGLIA SENDING THEIR PERIPHERAL PROCESSES INTO THE RAMI COMMUNICANTES

OTTORINO ROSSI

Clinic of Nervous and Mental Diseases of the University of Sassari

SEVEN FIGURES

During the last ten years our interest in studies concerning the sympathetic system has increased progressively, as clinical applications of the knowledge gradually acquired have become manifest. Consequently, there is an increasing number of investigators who carefully attempt to clarify the numerous problems of anatomy, physiology, and physiopathology which, up to the present time, are still under discussion in this intricate field.

Anatomists occupy themselves especially with two subjects of paramount importance. These are the connections of the sympathetic system and the origin and course of its afferent path. On the other hand, studies of the morphology of the sympathetic ganglion cells have decreased, since the description given by Cajal (1) by the aid of his silver method. Serious contributions to this subject have, however, appeared, of which I may be permitted to recall those of my pupil, Riquier (2), on the morphology of the cells of the ganglion oticum and the junction between spinal and sympathetic ganglia of the turtle.

In order to examine as closely as possible the two problems mentioned, anatomists, who follow to-day a procedure more and more biological, have been less inclined to employ direct observation of pictures which we are able to secure with present methods of staining normal nervous tissues than physiological experimentation and study of the changes produced by injuries to some portion of the sympathetic itself or other nervous structures which are supposed to be in relation with it.

The results which the English and American schools have secured by these methods are so well known that it is quite unnecessary to go into a detailed exposition and to assert that we expect great profit by their further use. Nevertheless, it seems to me that the study of pure anatomical preparations also should be able to give new contributions of value toward the solution of the complicated problems related to the sympathetic system. The researches of Müller (3) and his coworkers who have employed Bielschowsky's method and the Rongalitweiss-staining support my contention, which agrees also with the following findings concerning the question of the sensory sympathetic paths.

Lennander's idea that all visceral pain was mediated through the parietal peritoneum or through the sensory fibers of the visceral blood-vessels has been disproved, we may say, definitely by the majority of physiologists. At the present time two other views are under discussion about the pathways which convey visceral sensibility. The one, to-day widely accepted, assumes that all afferent sensory fibers present in the sympathetic nerves are peripheral processes of neurones the cell bodies of which lie in the spinal ganglia. Such special dorsal root neurones are believed to send their processes, via rami communicantes, into the sympathetic trunks, where they meet with and accompany the efferent postganglionic fibers to their terminations in tissues. According to such a view, visceral sensibility would be conveyed in pathways similar to those of the varieties of common sensibility, at least so far as concerns the afferent impulses of visceral origin which appear in consciousness. That is, sympathetic sensory structures are denied and it is affirmed that all the sympathetic elements are of motor character. The opposing view, supported by Dogiel and nowadays defended by the minority of neurologists, recognizes in the sympathetic mechanism sensory neurones which belong primarily to this system. These neurones would have their trophic centers in the various autonomic ganglia; their peripherally directed processes end in sensory terminal apparatuses of the viscera; their centrally directed processes run through the rami communicantes into the spinal ganglia

where they form terminal arborizations about some spinal ganglion cells, chiefly those of Dogiel's type II. The visceral impulses conveyed by these neurones are collected from spinal ganglion cells, the centripetally directed processes of which transmit them through the spinal cord upwards. Besides this long path, Dogiel assumes a shorter one which conveys those afferent visceral impulses which never rise into consciousness at all, but expend themselves in the production of peripheral reflexes; the centripetal fibers of many sensory autonomic cells are believed to end within sympathetic ganglia in connection with the dendrites of efferent cells. It will be here noticed that Dogiel's view does not necessarily deny the presence of afferent cerebrospinal fibers in the viscera.

It is not my purpose to cite all the discussions about the two foregoing views, discussions which we meet in every modern book about the sympathetic system, nor to recall the modifications of Dogiel's theory, which deserve more than a passing notice. The aim of my paper is merely to call attention to a definite anatomical finding which, in my opinion, gives a very valuable confirmation of the first view, but could not be used to disprove entirely the second.

The theory which assumes that the nerve cells from which arise the afferent paths of the sympathetic system lie in the spinal ganglia is based on physiological experimentation and on the following anatomical facts.

A. Morphological researches of Kölliker and Ramón y Cajal. These investigators have found some large nerve fibers coming off from the spinal ganglion and entering the ramus communicans. Kölliker assumed that these fibers formed the sensory sympathetic paths. Upon reading all of the literature available to me, I could not find that Kölliker or any other investigator has described the nerve cells from which arise those fibers which are commonly called Kölliker's fibers. In the account which Redlich wrote about Kölliker's lecture (4) we read: "jene freilich unklaren Empfindungen die wir normal von dem Zustande der vom Sympaticus versorgten Teile haben, leiten von der Funktion einer geringen Zahl dunkelrandiger Nervenfasern ab, die von

den sensiblen Wurzeln der Rückenmarksfasern durch die Verbindungsäste in den Grenzstrang des Sympaticus übertreten." When we consider these words and the influence that at such a time was exerted by the well-known experiments of C. Bernard and Bidder, we cannot but conclude that Kölliker not only was ignorant of the cells from which his large fibers take their origin, but also that he had not definitely disproved that they proceed from the spinal cord through the dorsal roots and traverse the spinal ganglia, as many workers believed. In his textbook Kölliker (5) assumes the existence of fibers which come off from the spinal ganglia, go through the rami communicantes into the sympathetic ganglia and continue to the periphery, but he does not say anything about the ganglion cells in which these fibers have their origin; only in his schema—reproduced, more or less modified, in all textbooks—does he picture them as arising from spinal ganglion cells of the common type.

Cajal (6) writes: "Certains auteurs, et parmi eux Kölliker, pensent que des fibres sensitives, nées dans les ganglions rachidiens, pénètrent dans le sympathique avec les rameaux communiquants blancs et ne font que traverser les ganglions sympathiques pour se terminer aux surfaces des muqueuses. Nous avons vu, nous aussi, dans l'embryon de poulet, des fibres épaisses, nées du ganglion rachidien voisin, entrer dans les ganglions du sympathique; mais le fait s'est présenté si rarement qu'il nous a été impossible d'étudier l'origine réelle et la terminaison de ces fibres."

Here reference might be made to the fact that Lenhossék (7) has shown that some fibers from the sensory roots enter the sympathetic ganglia, also that the sphenopalatine ganglion receives a bundle of nerve fibers from the gasserian ganglion, and further that some of the peripheral fibers of the geniculate ganglion enter the chorda tympani. Huber (8) believes that these sensory fibers do not end in the ganglia, as Lenhossék inclines to assume, but pass through the ganglia and become associated with the efferent sympathetic nerves. Huber met such medullated fibers which are larger than the preganglionic fibers in the frog's

bladder and traced them through two and through three small ganglia of the same bladder.

I did not succeed in finding in the literature anything more definite; therefore I believe that we are authorized to come to the conclusion that till now descriptive anatomy has not specified the origin of the so-called Kölliker's nerve fibers.

B. Experimental researches (Scaffidi (9)) show that injuries to the thoracic sympathetic ganglia led to distinct alterations of the stainable substance in the cells of the corresponding spinal ganglia, especially in some cells lying in the peripheral portion of the same.

C. Experimental researches demonstrate that in the rami communicantes albi are to be found large medullated fibers which fall into secondary degeneration only when cut off from the corresponding spinal ganglion, where consequently we must look for their trophic center.

Roux (10) cut, in the cat, anterior and posterior roots in the proximal tract (between spinal ganglion and spinal cord) and stated that many medullated fibers were to be found undegenerated in the corresponding ramus communicans. He further *routed out the spinal ganglion and verified the degeneration of* these fibers. From his own researches he came to the conclusion that the nerve cells from which the fibers mentioned arise are located in spinal ganglia.

Scaffidi (9) arrived at similar results and conclusions from analogous experiments, substituting, however, for the extirpation of the spinal ganglia a less injurious, more appropriate, operation. After having confirmed that cutting the proximal tract of the dorsal nerve root and the anterior root never produces degeneration of all of the medullated fibers of the ramus communicans, he cut the dorsal root caudad, viz., peripheral to the corresponding spinal ganglion, and so was able to see the degeneration of all the medullated fibers of the ramus communicans.

Of late Ranson and Billingsley (11), to whom the paper of the Italian investigator seems to have been unknown, performed similar experiments, but studied the preparations also by the

It is not necessary to emphasize the chief result of these researches. Though in the birds sometimes it is not easy to identify the ramus communicans by reason of its peculiar topographic relations, yet this is recognized clearly enough in the preparation from which is reproduced the first picture. Besides, I have met the same evidence in mammalian embryos.

Supported by my findings, of which I have pictured the most evident, the results afforded by my studies may be summarized as follows: *In embryos of birds and mammals there is demonstrated for the first time by direct anatomical observation the occurrence in the spinal ganglia of nerve cells the peripheral processes of which pass into the rami communicantes.*

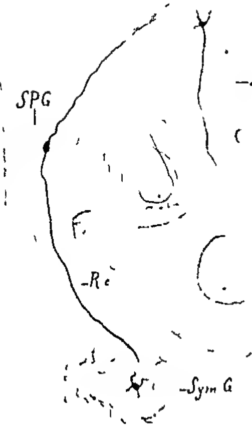
In my own preparations there is no evidence which could demonstrate that these nerve cells have peculiar character or position. One could perhaps question the constancy of such findings. I do not believe that they are occasional because in thirty well-impregnated bird embryos I met them more or less clearly fifteen times, and in thirteen pig embryos six times.

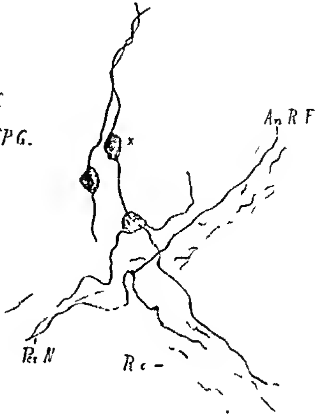
That previously illustrious investigators, such as Kölliker and Cajal, though successfully impregnating the processes, have not had the good fortune to impregnate their cells of origin, we can easily understand when we recollect all the circumstances which cooperate to modify the results of the wonderful method of Golgi, which is certainly able to give new and interesting findings about the relations of nerve cells when applied carefully and with sufficient persistence.

Fig. 1 Cross-section of embryo of Passer sardoa. Golgi's method. × 87. A spinal ganglion cell is seen sending its peripheral process into the ramus communicans. *R.c.*, ramus communicans; *Sp.C.*, spinal cord; *SP.G.*, spinal ganglion; *Sym.G.*, sympathetic ganglion.

Fig. 2 Cross-section of embryo of Passer sardoa. Golgi's method. × 267. Three nerve cells of the spinal ganglion send their peripheral processes through the ramus communicans. *Per.N.*, peripheral nerve; *R.c.*, ramus communicans; *Sp.C.*, spinal cord; *SP.G.*, spinal ganglion.

Fig. 3 Cross-section of embryo of Passer sardoa. Golgi's method. × 267. The spinal ganglion cell marked with a cross sends its peripheral process into the ramus communicans. One fiber of the anterior root (*An.R.F.*) divides at the level of the ramus communicans; one of the branches runs through the ramus itself. Other indications as in figure 2.





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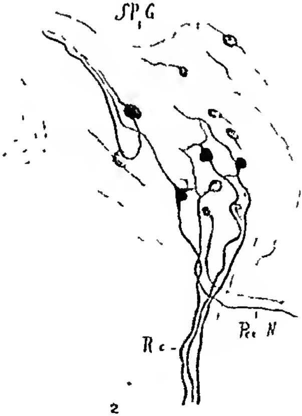

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The support which my findings give to Kölliker's view of the afferent sympathetic paths is clear. But they are not sufficient to disprove the possibility of the existenee of other sympathetie sensory paths. First, it is not certified by my observations where the peripheral processes arising from the deseribed spinal ganglion cells end. Seeond, reference may also be made to some reeent investigations performed with the method of seeondary degeneration and by direct anatomical observation which seem to demonstrate the oceurrenee of afferent sympathetic fibers the trophic centers of which lie in the sympathetie ganglia while the processes run through the rami eommunicantes and, according to many workers, reach the spinal ganglia. Here it will be notieed that Ranson and Billingsley found, in cat XIV, after section of the tenth thoraeic nerve distal to the spinal ganglion, a half-dozen normal myelinated fibers in the eorresponding white ramus, but they do not think that they are afferent fibers, the eells of origin of whieh lie in the sympathetie ganglion. On the eontrary, they believe that these may belong to a small gray ramus aeeompanying the white. It must also be mentioned that Müller, who saw some sympathetie fibers entering the spinal ganglion, supposed that they are postganglionie sympathetie fibers running through the ganglion to go off with the dorsal branch of the peripheral nerve. Sueh a view is supported by my finding reproduced in figure 7 (part of a eross-seetion of an embryo of Passer sardoa), where is shown a sympathetic nerve eell (*Sym.N.C.*) sending its postganglionic process through the corresponding spinal ganglion (*Sp.G.*) into the dorsal branch of the peripheral nerve (*D.B. P.N.*), to which runs also a fiber coming off from the anterior spinal root.

Finally, in the problem of visceral sensibility the anatomists must not forget the reeent physiologieal investigations of Lehmann, who believes that the viseeral sensory fibers run above all through the anterior spinal roots.

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